Modified forests are vital for species communities and ecological functionality in a heterogeneous South African landscape

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I. General introduction

Forest loss in a human-modified world

During the last decades, the world has faced an unprecedented decline of global forest cover. In particular, tropical and subtropical forests have been threatened by changes in human land-use, finally resulting in an extensive loss of biodiversity (Vitousek et al. 1997; Lewis 2006; FAO 2011). Although many scientists over the past years have turned their attention to the worldwide forest decline, we still remain with uncertainties. Estimates on the current extent of deforestation, for example, vary immensely and future scenarios on the prospective forest cover are even more ambiguous (Lewis 2006; Wright and Muller-Landau 2006). There is, however, consensus that we expect a vast increase of human-modified forests on earth. This leads to a controversial discussion on how far modified forests can compensate for the loss of natural forests and thus, whether they sustain biodiversity and the ecosystem functionality of natural forest (Wright and Muller-Landau 2006; Barlow et al. 2007; Laurance 2007; Gardner et al. 2009). The disagreement on the role of modified forests might be based on the difficulty to generalize the magnitude of human impacts. Even though it has been suggested that forest modification may cause overall shifts in species richness, community composition and species interactions (Chapin et al. 2000), we still lack studies that itemize the effects of different facets of human forest modification on species communities and their ecological functionality. As ongoing human impact will further turn tropical and subtropical forests into mosaics of differently disturbed habitat, it is of major importance to evaluate the consequences of forest modification at a landscape scale.

Pollination in human-modified landscapes

About 95% of the tropical angiosperms depend on animals that disperse their pollen and thus, facilitate regional gene flow (Ollerton et al. 2010). Consequently, pollination services are critical for the successful reproduction and long-term persistence of plant populations (Bawa 1990; Didham et al. 1996; Ollerton et al. 2010). There is serious evidence that land-use intensification fosters a decline of pollinating insects in fragmented forests (Aizen and Feinsinger 1994). The consequences of a pollinator decline, however, are hotly debated. Some scientists assume that the loss of single species may not be relevant for the viability of plants (Cane et al. 2006). Further studies underline the resilience of pollination processes and suggest that most likely, some pollinators may undertake the role of others (Ghazoul 2005; Ghazoul and Koh 2010). In contrast, some authors caution that a decline of pollinators may substantially affect pollination services (Aizen and Feinsinger 1994). Whereas numerous studies have investigated the effects of anthropogenic impacts on pollination services of crop plants (e.g., Kremen et al. 2002; Chacoff and Aizen 2006), fewer studies have addressed natural pollination systems of tropical or subtropical forest trees (but see e.g., Dick et al.

2003) and only a handful of these involve a broad range of different forest disturbance intensities (e.g., Aizen and Feinsinger 1994). Therefore, we lack comprehensive studies on different intensities of forest modification to understand the effects of anthropogenic impact on pollinators and pollination services.

Seed dispersal in human-modified landscapes

Seed dispersal is one of the key aspects in a plant's life-cycle. Various seed dispersal mechanisms have evolved, including abiotic vectors such as dispersal by wind or water and biotic vectors such as dispersal by animals (Howe and Smallwood 1982). In particular in tropical regions, where more than 90% of trees bear fleshy fruits, plant-frugivore interactions are of great importance (Howe and Smallwood 1982). Frugivorous birds, for instance, provide important dispersal services as they can carry swallowed seeds even to remote areas far away from the mother plant (Holbrook and Smith 2000; Sekercioglu 2006). Gut passage may facilitate or even induce germination processes once a seed has reached its final destination (Howe and Smallwood 1982).

Acknowledging the strong dependency of many plants on their seed dispersers, it is not surprising that a loss of seed dispersing frugivores may strongly affect plant regeneration processes (Cordeiro and Howe 2001; Howe and Miriti 2004; Terborgh et al. 2008). Seed disperser decline in turn hampers plant recruitment and therefore increases the probability of local extinction of plant populations (Forget and Jansen 2007; Terborgh et al. 2008; Holbrook and Loiselle 2009). This is in particular true for human-modified forests, where hunting and overexploitation often cause a decline of fruit-eating animal populations. In contrast, other studies have suggested that structurally rich modified forests can maintain high frugivore richness (Ranganathan et al. 2008). Mobile frugivores, such as birds that use forest remnants as sources for food, can significantly increase seed rain in abandoned agricultural areas (Au et al. 2006). Despite their important role for forest regeneration, we still lack information on how frugivorous birds respond to different intensities of forest modification. Thus, investigating the effects of human impact on bird communities and seed dispersal in heterogeneous forest landscapes is an important task for conservationists.

Bird movements in human-modified landscapes

Birds are supposed to maintain the most diverse range of ecological functions among vertebrates. Due to their mobility they act as "mobile links" providing important ecological services for many plants at a landscape scale, such as pollination or the dispersal of seeds (Sekercioglu 2006). Despite their physical capability to cross hostile matrix habitat, studies on the abilities of birds to disperse among forest patches within human-modified landscapes

are rather contradictory (Price 2006; Lees and Peres 2009; Hansbauer et al. 2010). While landscape characteristics may strongly determine bird movement behaviour (Graham 2001; Gillies et al. 2011), bird functional traits, such as body size, dietary or habitat specialization, are important to predict a bird's movement ability across a landscape (Lees and Peres 2008; Gillies and St Clair 2010). Consequently, the ecological grouping of birds according to quantitative and qualitative species traits may help to understand general movement patterns of bird assemblages. Although the movements of single bird species across heterogeneous landscapes are well studied (e.g., Graham 2001; Hansbauer et al. 2008; Gillies et al. 2011), extensive community-based studies are scarce. Yet, merging the responses of bird functional groups at a community level will help to understand the effects of landscape modification on bird assemblages and their ecosystem functionality.

Outline of the thesis

In the present thesis, I investigated the effects of forest modification on insect and bird communities along a gradient of different disturbance intensities. Further, I studied two fundamental ecological services – pollination and seed dispersal. To assess how forest modification affects the dispersal of animals, I carried out an in-depth study on the movement behaviour of bird assemblages across a fragmented landscape. These comprehensive studies shall help to understand the effects of forest configuration on species communities and ecosystem functionality at a landscape scale.

Study area

All studies presented in this thesis were conducted on the East coast of KwaZulu-Natal, South Africa. Historically, this region has been characterized by patches of indigenous scarp forest, interspersed in natural grassland vegetation (Cooper 1985). However, deforestation and agricultural intensification have strongly diminished the total scarp forest cover during the last decades (Eeley et al. 2001). Only few undisturbed scarp forests are maintained, mainly restricted to nature reserves and conservation areas. The remaining scarp forests are of high conservation priority on account of their biodiversity and the degree of endemism (Eeley et al. 2001; von Maltitz 2003). I conducted my studies in the two protected areas Oribi Gorge and Vernon Crookes. These nature reserves contain two of the largest, undisturbed areas of continuous scarp forest (von Maltitz 2003). Beyond the borders of Vernon Crookes and Oribi Gorge, the region is dominated by intensive agricultural farming, such as sugar cane and eucalyptus plantations. However, numerous unprotected and privately owned scarp forest fragments remain in the human-modified landscape. Different intensities of anthropogenic disturbance have strongly affected most of these forest remnants, forming a heterogeneous

mosaic of differently modified scarp forest patches at the landscape scale. I selected the six most representative types of scarp forest modification that were present in the region representing a gradient of intensification. These included undisturbed, continuous forest and natural forest fragments within nature reserves, as well as patches of native forest located in eucalyptus plantations and sugar cane fields. Additionally, I included large, forested farm gardens as a type of forest modification, as they resemble indigenous forest patches in the agricultural landscape. Lastly, forest patches in privately owned game reserves, strongly impacted by game and cattle grazing, represent a secondary scarp forest type. To quantify the magnitude of human impact, I selected canopy cover as a continuous variable to measure the degree of forest modification and human disturbance in the different forest types (Harvey et al. 2006).

Objectives

The purpose of this dissertation was to investigate the effects of different intensities of scarp forest modification on flower-visiting insect and bird communities and their ecological functionality in a human-modified landscape.

Chapter **II** of this thesis reports on a study that investigates the effects of forest modification on overall insect flower visitor assemblages and flower visitation on the native tree *Celtis africana* (Ulmaceae) in 36 study sites of six different forest types. I focussed on *C. africana*, as this common and generalist tree is largely able to persist in modified forests and thus, represents an optimal focal species to compare plant-animal interactions in a landscape context. My aim was to investigate how potential shifts in the overall insect flower visitor community among the different forest types translate into changes in the visitation rates to *C. africana* flowers and ultimately, in fruit set.

Chapter **III** deals with a project investigating the effects of forest modification on bird community composition and seed removal of *C. africana* in the same six forest types. Here, I aimed to investigate whether human disturbance affects forest specialist species more strongly than generalists, resulting in shifts in bird species composition among the forest types. Furthermore, I intended to find out whether frugivore visitation which supports seed-removal services at *C. africana* is maintained in modified forests.

Finally, chapter **IV** is concerned with a study on the movement behaviour of bird assemblages across nine forest patches of three different forest types. In this study, I aimed to investigate how species traits and forest configuration shape the movement activity of both birds that conduct long-distance movements across the landscape and "resident" birds that conduct only short movements within a particular forest fragment.

Chapters **II**, **III** and **IV** of this thesis have been published or are submitted to journals. Thus, they represent closed entities than can be read independently of each other.

Pease note that in some cases, this might lead to redundancy in the content among the different chapters.

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II. Resilience of insect assemblages and flower visitation of a generalist tree in modified forests

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Abstract

Flower-visiting insects provide essential pollination services to many plant species. It is thus of critical importance to understand the effects of anthropogenic landscape modification on these animals. Particularly at the landscape scale, we still lack information on how pollinator assemblages are affected by different intensities of human disturbance. In this study, we chose six representative types of forest modification across a heterogeneous South African landscape. At 36 study sites we assessed flower visitors using insect traps and direct observations of insect visitation to *Celtis africana* flowers. This generalist tree species has small unspecialized flowers, which we found to be pollinated by a diverse array of insects as well as by wind. Rarefied flower visitor richness, community composition and visitation rates to *C. africana* differed significantly among the different forest types and between two study years. Flower visitor richness and visitation rates to *C. africana*, were enhanced in modified forests, the latter facilitated by a high abundance of large-bodied pollinators. Nevertheless, effective fruit set in *C. africana* was not significantly correlated with insect visitation across the various forest types. Procrustes analyses of insect assemblages and the tree community revealed that both were positively associated. Our findings imply that even though forest modification can strongly alter insect assemblages, pollination services for trees with unspecialized flowers may remain resilient at a landscape scale. We advise conservation managers to maintain modified forest fragments as these are pivotal to sustain pollination services in human modified landscapes.

Introduction

Deforestation and forest modification by humans threaten forest ecosystems worldwide (Lewis 2006). Although estimates of current deforestation rates vary immensely (Wright and Muller-Landau 2006), future scenarios predict a further decline of the global forest cover, increasing modification of forest habitats, and at the same time a dramatic loss of biodiversity (Lewis 2006). Numerous studies have shown that forest disturbance negatively affects species richness and ecological processes (e.g., Larsen et al. 2005; Lewis 2006; Gardner et al. 2009). On the other hand, a number of studies suggest that modified and secondary forests can maintain high species richness that provides essential ecological services such as pollination or seed dispersal (Dick et al. 2003; Farwig et al. 2006; Winfree et al. 2007; Quintero et al. 2010; Neuschulz et al. 2011). As ongoing human disturbance gradually converts existing forests into local mosaics of modified forest habitats (Gardner et al. 2009), future research needs to disentangle the effects of different disturbance intensities on species communities and their ecological services in human modified landscapes.

Pollination by animals is regarded as one of the most essential ecological services, providing regional gene flow and hence, maintaining natural plant viability and the long-term persistence of plant populations (Didham et al. 1996; Kearns et al. 1998; Dick et al. 2003; Ollerton et al. 2010). In fact, estimates suggest that about 87% of angiosperms globally depend on biotic pollination (Ollerton et al. 2010). At the same time, pollinators depend on the floral rewards presented by many plants as food sources (Kearns et al. 1998). This mutualism potentially makes plant-pollinator interactions sensitive to human-induced disturbances, which, ultimately, may affect ecosystem functioning (Larsen et al. 2005) and global crop production (Kremen et al. 2002; Larsen et al. 2005). Previous studies have shown that anthropogenic disturbance can lead to considerable changes in insect pollinator communities (e.g., Samejima et al. 2004; Tylianakis et al. 2005), pollination of single plant species (e.g., Ward and Johnson 2005; Cane et al. 2006), and plant-pollinator networks (Hagen and Kraemer 2010). Functional traits such as body size, the trophic position, social behaviour, or the degree of specialisation on habitat or food sources may strongly influence the ability of pollinators to persist in anthropogenic habitats (Steffan-Dewenter et al. 2002; Schweiger et al. 2005; Cane et al. 2006) and thus, might structure overall pollinator communities and pollination services at a landscape scale. While large-bodied pollinators, for instance, show good dispersal abilities and wide foraging ranges, small pollinators are more restricted in their movement abilities and thus, depend on the availability of local habitat rather than on large-scale landscape structure (Gathmann and Tscharntke 2002). Eventually, differences in the functionality of pollinators may cause resilience of pollination processes as

it is likely that some pollinators may undertake the role of others (Ghazoul 2005; Cane et al. 2006; Ghazoul and Koh 2010).

Whereas numerous studies have investigated the effects of anthropogenic impacts on the pollination of crop plants (e.g., Kremen et al. 2002; Klein et al. 2003; Ricketts 2004, Chacoff and Aizen 2006), fewer studies have addressed natural pollination systems of tropical or subtropical forest trees (but see e.g., Dick et al. 2003; Cane et al. 2006), and only a handful of these involve a broad range of different forest disturbance intensities (but see e.g., Aizen and Feinsinger 1994). In the present study we asked whether anthropogenic forest modification within a heterogeneous subtropical landscape affects (1) overall insect flower visitor assemblages and (2) the pollination of the native tree *Celtis africana*. To address these questions, we compared the richness and the composition of insect flower visitor assemblages among six representative types of forest modification, influenced by different intensities of human disturbance. Further, we investigated the flower visitation by insect flower visitors to *C. africana* trees at the same forest types. We hypothesized that shifts in the overall insect flower visitor community among the different forest types may directly translate into changes in the visitation rates to *C. africana* flowers and ultimately, in fruit set. As body size is considered to be closely related to the dispersal ability of insect flower visitors, we expected an increase of large-bodied insect flower visitors in the modified forest fragments.

Materials and Methods

Study area and design

We conducted our studies from August to October 2009 and 2010 in Vernon Crookes (VC) (30°16'S, 30°35'E, 2189 ha) and Oribi Gorge (OG) (30°40'S, 30°18'E, 1850 ha) Nature Reserve and the surrounding area in KwaZulu-Natal, South Africa (Appendix chapter II A.1). The natural vegetation of the region is characterised by grassland and scattered patches of indigenous scarp forest, which is considered to be of conservation priority on account of its biodiversity and the degree of endemism (von Maltitz 2003). However, the few undisturbed scarp forests are rare and mainly restricted to nature reserves and conservation areas. Beyond the borders of protected areas, anthropogenic disturbance strongly modifies the remaining forests. We selected the six most representative types of scarp forest modification in our study region, characterised by different intensities of human impact (Appendix chapter II A.1). As dense canopy cover has been suggested to be an important measure of disturbance (e.g., Kirika et al. 2008), we used this criterion to classify the six representative forest types:

1) Continuous natural forests (NFor, mean canopy cover 64% ± 10.0 SE): the largest continuous forests that were found within VC and OG Nature Reserve. The sizes of the forest blocks were 130 ha (VC) and 822 ha (OG).
2) Small natural forest fragments (NFra, 66% ± 11.9 SE): forest islands within VC Nature Reserve formed by microclimatic and terrain conditions (mean size of the fragments: 2.3 ha ± 0.9 SE).
3) Forest fragments in timber plantations (PFra, 44% ± 3.7 SE): small stretches of native tree species that remained within eucalyptus plantations, mostly close to river beds.
4) Forest fragments in the agricultural matrix (AFra, 34% ± 8.0 SE): forest islands surrounded by extensive sugar cane fields, the predominant crop in the study region (mean size of the fragments: 3.2 ha ± 0.7 SE).
5) Forested gardens (FGar, 28% ± 5.0 SE): private farm house gardens surrounded by an agricultural matrix and shaped by a mixture of old and recently planted native tree species and ornamental plants.
6) Secondary forests (SFor, 1% ± 0.8 SE): located in private game reserves characterised by a distinct shrub cover (20%) with predominant *Acacia* species due to decades of heavy game and cattle grazing. Due to the close vicinity to VC and OG Nature Reserve and thus, similar terrain and climate conditions, we expect scarp forest as the original natural vegetation.

We established 36 plots (50 × 50 m) including 6 replicates in each forest type. Each plot contained at least one flowering *C. africana* tree. The minimum distance between the plots was 500 m, except for the plantation sites, which were at least 200 m apart from each other. Because different forest types were not evenly distributed over the two study regions, replicate plots of most forest types were spatially clustered. However, both study regions VC and OG were located in the natural range of occurrence of scarp forests, characterised by similar soil and climate conditions (Cooper 1985; von Maltitz 2003) as well as land-use intensity. Thus, natural environmental gradients were clearly negligible compared to the differences among forest types caused by human modification.

Study species

The monoecious deciduous native tree *Celtis africana* (Ulmaceae) is largely able to persist in human modified forest habitats. Hence, it represents an optimal species to compare pollinator activity among the six forest types. The flowers occur before leaves emerge and are predominantly unisexual with occasional hermaphrodites being produced. A group of c 10 male flowers usually surrounds one to four female flowers, all together forming a cluster of flowers which we will denote in the following as a flowerhead. Male and female flowers are < 5 mm small, yellow to greenish and attract a variety of different insects (Coates Palgrave 2005).

Assemblages of flower-visiting insects

We assessed assemblages of insect flower visitors in September 2009 and 2010. Five butterfly traps, baited with fermented fruit, were randomly placed within each study plot. Additionally, we established three stations of pan traps per study site, consisting of one yellow, one white and one blue pan trap filled with soapy water and glycerine. All traps were left open for 24 hours. To account for different weather conditions of the sampling days, we captured insect flower visitors simultaneously in at least three different forest types. No sampling was conducted under rainy weather conditions. To exclude all non-pollinating insects captured by the traps, we only selected insects of the orders Diptera, Hymenoptera, Lepidoptera and Coleoptera from which generally most pollinators are drawn. Insects were identified to family level according to Scholtz and Holm (2008) and afterwards classified into morphospecies, in the following referred to as species. Classification into morphospecies can only be used as a proxy for the overall insect flower visitor richness and might not reflect the actual species occurrence. Nevertheless, this method allows an adequate comparison of the insect flower visitor assemblages among the different forest types (Oliver and Beattie 1996).

Flower visitation

We investigated the activity of flower visitors on *C. africana* flowers in August and September 2009 and 2010. Each of the 36 study trees was observed ten times for 20 minutes over the whole flowering season. In 2010 we had to reduce the sample size to 34 trees, as two study trees were past flowering at the time of observation. For each observation we focused on a flowering branch in the tree crown using a spotting scope. Five to 15 flowers were selected for which we recorded all flower visitors. We noted the number of flowers visited and the duration time per flower for each visitor. As species identification is prone to be inaccurate over long distances in the field, we used a combination of size determination and classification into morphospecies. The body size of each visitor was estimated and classified into four size classes: (1) < 2 mm, (2) 2 – 5 mm, (3) 5 – 10 mm, and (4) > 10 mm. Finally, we classified 20 different morphospecies pollinating *C. africana* (Appendix chapter II A.2). We pooled all observations per study tree of each study year and calculated the mean insect visitation rate per flower within 20 min for each study tree. Furthermore, we calculated the mean duration time of each visitor per flower. To asses the frequency of flower visitation of each insect group, we divided the number of flowers visited by a particular insect group by the total number of flowers observed.

For each study tree we recorded stem diameter at breast height (dbh) and flower display at the time of observation as well as the overall flower availability of flowering trees and shrubs of any species within a radius of 25 m around the study tree. After each flowering season we estimated the overall fruit set of each study tree. To compare the fruit set of different study trees varying in size and flower display, we calculated the effective fruit set for

each study tree by dividing the total number of fruits by the maximum number of flowers recorded.

Pollination experiments

We conducted controlled pollination experiments on *C. africana* over the two study years to determine whether fruit production can be increased by supplemental cross-pollination, whether wind pollination is possible and whether plants are capable of autogamous fruit production. We selected 14 *C. africana* trees from all six forest types and applied four different pollination treatments. 1) We pollinated all receptive stigmas of one flower by hand using anthers from male flowers of at least three different pollen fathers and bagged the flower after pollination. 2) We left flowers open to determine fruit production under natural pollination. 3) To assess the possibility of wind-pollination, we excluded insects using bags of large mesh size (~ 200 µm, diameter of *C. africana* pollen: ~ 27 µm) that has been shown to exclude insects, but allow pollination by wind. 4) We tested whether fruits could be produced in the absence of wind or insect pollination using fine-mesh pollination bags that excluded insect- and wind pollination. Each treatment was replicated on 2 – 6 flowers at the particular study tree. To calculate the experimental fruit set, we counted all fruits of the flowers at the end of each study period and divided them by the number of treated flowers.

Statistical analysis

For all analyses we used forest type as the categorical predictor. We tested the effect of forest type on rarefied richness of insect flower visitors (square root- transformed) for both years using Repeated Measures Analysis of Variance (RM ANOVA). Species rarefaction is an appropriate method to estimate whether sampling was sufficient to approach the asymptote of overall species richness. Differences in the composition of the four insect orders (arcsine square root-transformed) among the forest types were analysed using Multivariate Analyses of Variance (MANOVAs) for both years separately. Moreover, we tested whether the community composition of insect flower visitors could be explained by the tree species composition at the study plots. We used data from a previous study that recorded all woody trees and shrubs with a maximum height of 4 m at 500 m² within each plot. As only 26 study plots (five NFor, five NFra, six PFra, four AFra, and six SFor) coincided with the present study, we reduced the data set for this analysis. We used Non-metric Multidimensional Scaling (NMDS) of the insect flower visitor and tree communities followed by orthogonal, least-squares Procrustes rotation as implemented in Vegan 1. 17-3 (Oksanen et al. 2010). Procrustes analysis is a powerful tool for correlating two matrices to fit the other followed by permutation tests to determine significances (Jackson 1995; Alarćon 2010). We converted the resulting m² statistic as a measure of goodness-of-fit to the percentage of congruence between the two matrices to facilitate interpretation as suggested by Alarćon (2010). We

obtained vector residuals for each study plot as a measure of the deviation between two particular data points of each matrix. Finally, we tested whether the concordance of insect flower visitor and tree matrices differed among the forest types in both years using ANOVAs.

We tested whether the mean flower visitation rates of *C. africana* differed among forest types in both years using RM ANOVA. Furthermore, we tested for differences in the mean flower visitation rate (log-transformed) among the forest types for each year separately using ANOVAs and Analyses of Covariance (ANCOVAs) followed by Tukey's HSD multiple pairwise comparisons. We included flower display, mean dbh of *C. africana* trees, and overall flower display of the surrounding flowering trees and shrubs (all log-transformed) as predictor variables with stepwise deletion of non-significant terms ($p > 0.05$). Differences in the composition of the four size classes (square root-transformed) among the forest types were analysed using MANOVAs. We tested the effect of forest type on the mean duration time per flower and the mean visitation frequency of the insect flower visitors including the size of the flower visitors as categorical predictor. Due to the nested structure of this model we included the study site as an error term. Here, we present the data of 2009 only, though results were similar in both years. Finally, we tested whether the forest type had an effect on the effective fruit set (arcsine square root-transformed) including mean flower visitation rate (square root-transformed) as a predictor variable using ANCOVAs.

We used a Generalized Linear Mixed Model (GLMM) to test the effects of the different pollination treatments on fruit set including the study tree as a random factor. The response variable proportion of fruit set was modelled following a binomial error distribution. Differences among pollination treatments were compared using Tukey's HSD multiple pairwise comparison. All analyses were conducted in R (R Development Core Team 2010).

Results

Insect flower visitor assemblages

Over the two years we recorded a total of 11,590 insects belonging to Diptera, Hymenoptera, Lepidoptera, and Coleoptera, which we classified into 290 different morphospecies. We detected significant differences in rarefied insect flower visitor richness among the six forest types and the two sampling years (Table 1). The rarefaction curves of all study sites converged to saturation, indicating that the sampling was adequate for assessing the overall insect flower visitor richness in the different forest types (Fig. 1). In both years, insect flower visitor richness was highest in secondary forests, forested gardens and fragments within agriculture, even though the latter showed a much lower richness in 2009 than in 2010 (Fig. 1). Relatively low insect flower visitor richness was recorded in natural forests, natural forest fragments and fragments within plantations. The composition of the orders Diptera, Hymenoptera,

Lepidoptera, and Coleoptera varied significantly among the six forest types in both years (MANOVA: Pillai $_{5,30}$ = 0.88, p = 0.042 (2009), Pillai $_{5,30}$ = 1.16, p = 0.002 (2010)).

Table 1. Repeated Measures ANOVAs of the rarefied insect flower visitor richness and the flower visitation to C. africana (both square root-transformed) as a function of forest type and study year (2009 and 2010).

Rarefied insect flower visitor richness	df	F	p
Forest type	5,30	4.04	0.006 **
Year	1,30	19.04	<0.001 ***
Forest type × year	5,30	0.62	0.686 ns
Flower visitation	df	F	p
Forest type	5,28	3.06	0.025 *
Year	1,28	55.27	< 0.001 ***
Forest type × year	5,28	6.71	< 0.001 ***

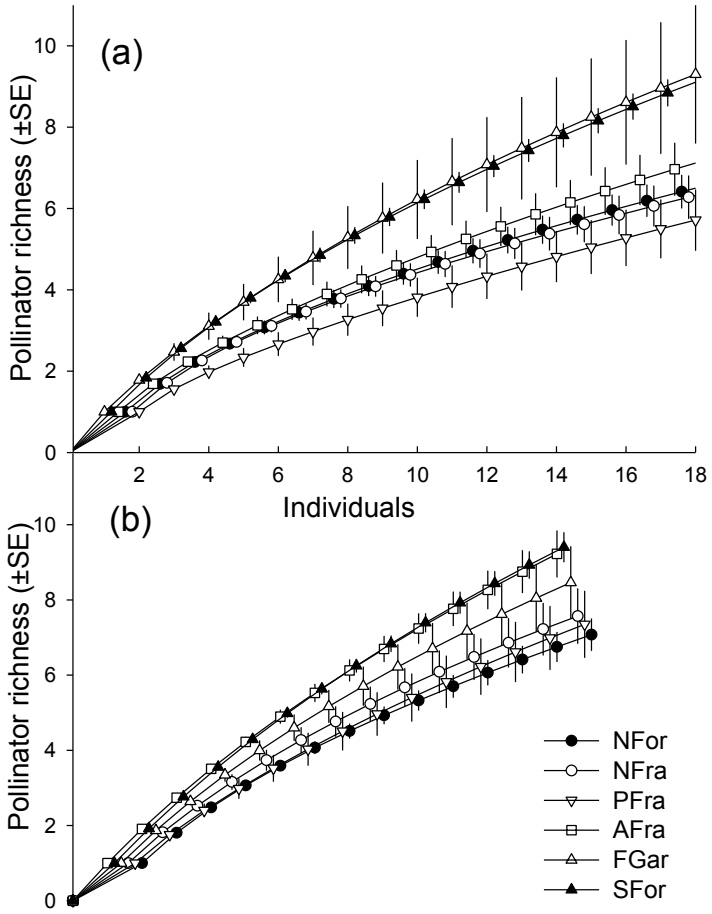

Fig. 1. Individual-based rarefaction curves displaying insect flower visitor richness in a) 2009 and b) 2010 in the six forest types: continuous natural forests (NFor), natural forest fragments (NFra), fragments within plantation (PFra), fragments within agriculture (AFra), forested gardens (FGar), and secondary forests (SFor). Symbols are slightly displaced at the x- axis to improve readability.

Procrustes analyses of the insect flower visitor assemblages and the tree community revealed that both were positively associated. In 2009 the congruence between both matrices was 46% ($m^2 = 0.54$, $p < 0.001$) whereas congruence was only 30% in 2010 ($m^2 = 0.70$, $p = 0.001$). Mean vector residuals did not vary significantly among the different forest types in both years, indicating that the concordance between the matrices were similar for all forest types (2009: $F_{4,21} = 2.06$, $p = 0.123$; 2010: $F_{4,21} = 1.09$, $p = 0.387$).

Flower visitation

C. africana flowers were mainly visited by flies (45%), followed by honey bees (40%), hoverflies (8%), and wasps (5%, Appendix chapter II A2). Total visitation rates dropped by more than 60% from 0.69 visits per flower in 2009 to 0.26 visits per flower in 2010 (Fig. 2). Hence, the differences in insect flower visitation rates were highly significant between the two years (Table 1). Furthermore, we detected significant differences among the forest types in the visitation rates over both years (Table 1). In 2009 the highest visitation rates were recorded in forested gardens which differed significantly from the lowest visitation rates detected in natural forests and natural forest fragments ($F_{5,30} = 6.19$, $p < 0.001$). Intermediate visitation rates were detected in fragments within agriculture, fragments within plantations and secondary forests. The effect of forest type on insect visitation rates was only marginally significant in 2010 ($F_{5,28} = 2.32$, $p = 0.069$) as visitation rates were equally low in all forest types despite relatively high visitation rates in fragments within plantations. None of the predictor variables contributed significantly to the models and thus, all variables were excluded.

The composition of the four size classes varied significantly among the different forest types (MANOVA: Pillai $_{5,30} = 1.05$, $p = 0.007$ (2009), Pillai $_{5,28} = 1.16$, $p = 0.003$ (2010), Fig. 2). A greater proportion of large-bodied insect flower visitors (> 10 mm) visited forested gardens, fragments within plantations and agriculture in both years, as well as secondary forests in 2009 (Fig. 2). Feral honey bees accounted for 94% of these large insect flower visitors and thus, constitute the prominent visitation rates in the modified forest types. Different sized insect flower visitors differed significantly in their behaviour, which was not significantly affected by forest type (Table 2). While insect flower visitors of the sizes 2 – 5 mm and 5 – 10 mm had a significantly longer duration time per flower, the duration time of the smallest (< 2 mm) and the largest (> 10 mm) insect flower visitors were relatively short (Fig. 3a). The frequency of flower visitation was highest for insect flower visitors of 5 – 10 mm size and differed significantly from rather low visitor frequencies of the sizes < 2 mm and > 10 mm (Fig. 4b). The effective fruit set of each *C. africana* tree was not affected by forest type, flower visitation rate and the interaction of forest type and visitation rate in both study years (ANCOVA whole model 2009: $F_{11,24} = 1.26$, $p = 0.304$, forest type: $F = 1.84$, $df = 5$, $p = 0.142$, visitation rate: $F = 0.03$, $df = 1$, $p = 0.872$, forest type × visitation rate:

F = 0.93, df = 5, p = 0.482; Whole model 2010: $F_{11,22}$ = 1.24, p = 0.319, forest type: F = 0.18, df = 5, p = 0.162, visitation rate: F = 0.37, df = 1, p = 0.550, forest type × visitation rate: F = 0.90, df = 5, p = 0.501).

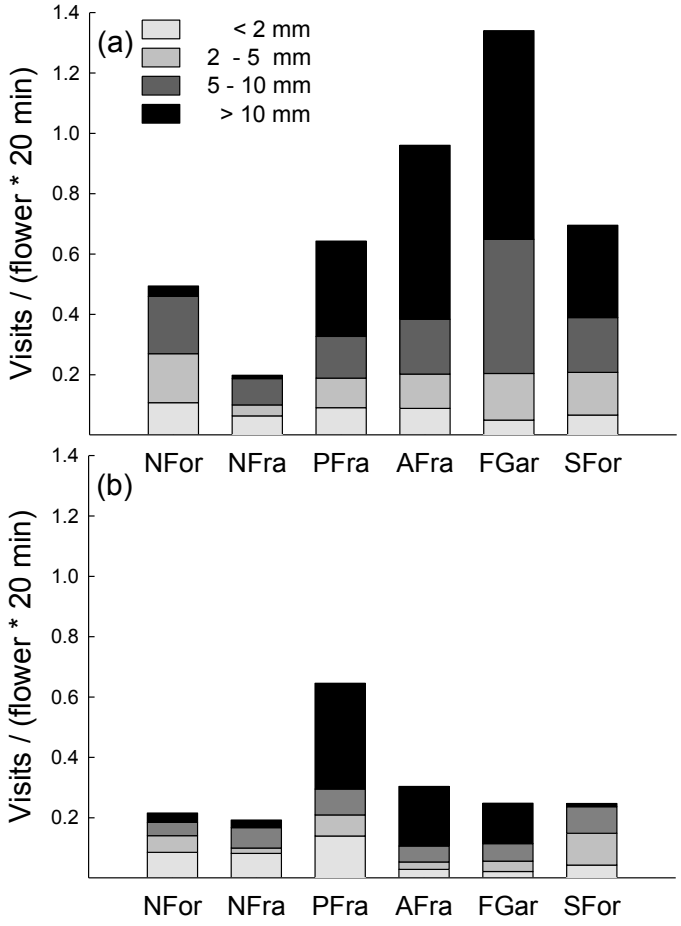

Fig. 2. Mean visitation rates of different insect size classes observed on *C. africana* flowers within 20 min in a) 2009 and b) 2010 in the six forest types: continuous natural forests (NFor), natural forest fragments (NFra), fragments within plantation (PFra), fragments within agriculture (AFra), forested gardens (FGar), and secondary forests (SFor).

Table 2. Nested ANOVAs of the duration time per flower, and the frequency of flower visitation to *C. africana* (both square root-transformed) in 2009 as a function of forest type and insect size class. The study site was included as error term.

Duration per flower	df	F	p
Forest type	5,30	1.25	0.309 ns
Size	3,90	29.55	< 0.001 ***
Forest type × size	15,90	0.82	0.656 ns
Frequency of flower visitation	df	F	p
Forest type	5,30	0.79	0.569 ns
Size	3,90	9.53	< 0.001 ***
Forest type × size	15,90	1.75	0.055 ns

Pollination experiments

Experimental pollination success differed significantly among the four treatments (GLMM: fixed effect (treatment): $\chi^2_{3,10} = 45.72$, $p < 0.001$. Highest seed set was achieved by hand pollination (raw mean: 64.9% ± 6.0 SE, n = 14) followed by open pollination (47.4% ± 9.6 SE, n = 14), and wind pollination (34.1% ± 8.7 SE, n = 14). Lowest seed set was recorded in the complete exclusion treatment (11.4% ± 6.9 SE, n = 5). Hand pollination significantly increased seed set compared to insect pollination ($p = 0.001$), wind pollination ($p < 0.001$), and autonomous fruit production ($p < 0.001$). The difference in fruit set between flowers in the open and complete exclusion treatments was also significant ($p = 0.009$). All other differences were not significant.

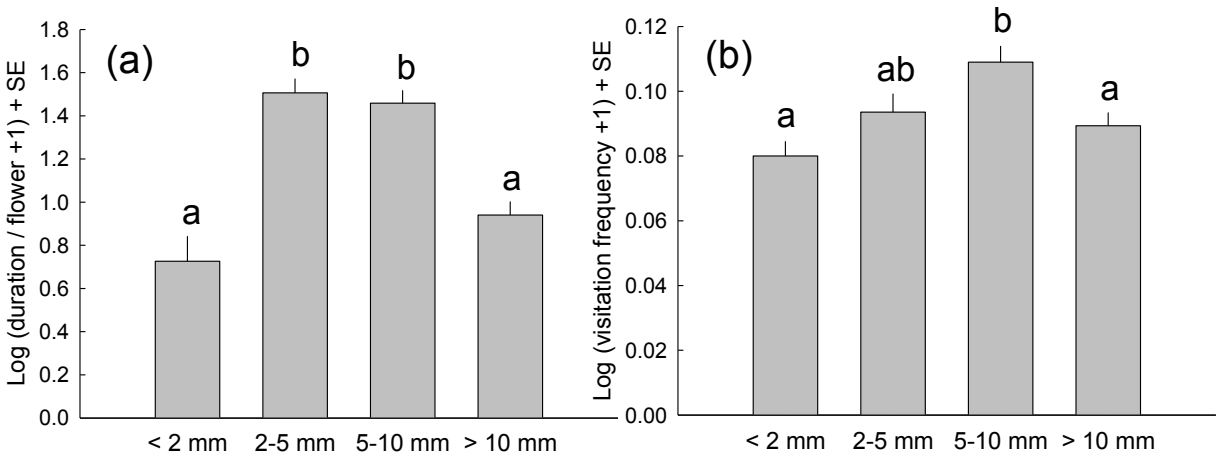

Fig. 3. a) Duration time per flower, and b) frequency of flower visitation (both log-transformed) of different insect size classes visiting *C. africana* trees. Shown are least square means (+ SE), different letters indicate significant differences among forest types according to Tukey's HSD multiple pairwise comparison.

Discussion

Insect flower visitor assemblages

The rarefied richness of insect flower visitors differed significantly among the different forest types. We detected higher rarefied richness in modified forests than in natural forest types. This effect persisted even though we detected highly significant variability between the insect flower visitor richness of both study years. Previous studies confirm strong effects of human impact on insect flower visitor assemblages (Didham et al. 1996) but the magnitude is difficult to predict (Quintero et al. 2010). While some studies are in line with our results (e.g., Liow et al. 2001; Winfree et al. 2007; Quintero et al. 2010), other studies recorded a decline of insect flower visitor richness in human disturbed forests (Aizen and Feinsinger 1994; Didham et al. 1996; Tylianakis et al. 2005) or no effect of habitat modification on insect flower visitor richness (Brosi et al. 2008). Despite the complexity of pollinators' responses to human disturbance, most studies have recorded strong compositional shifts of the overall community caused by habitat modification (e.g., Aizen and Feinsinger 1994; Liow et al. 2001; Winfree et al. 2007; Quintero et al. 2010). Accordingly, forest type had a significant effect on the composition of Diptera, Hymenoptera, Lepidoptera, and Coleoptera in both years. Our results indicate that shifts in the insect flower visitor community composition might have been driven by altered tree species composition in the different forest types. These findings are consistent with previous studies showing that insect flower visitors may strongly be affected by changing forest structure as for instance the composition of flowering plant species (Potts et al. 2003) or the density of large trees (Liow et al. 2001), which provide suitable nesting sites (Samejima et al. 2004). Further factors, such as microclimate or historical land-use are suggested to considerably affect insect flower visitor assemblages (Liow et al. 2001; Potts et al. 2003; Cane et al. 2006). Consequently, the magnitude of human impact on insect flower visitor assemblages seems to depend on a complex interaction of local disturbance intensities and environmental factors.

Despite the differences we detected in the insect flower visitor community among the forest types, we found a large variability in the rarefied richness among both study years. Large fluctuations are a common phenomenon in insect populations (Roubik 2001; Ricketts 2004; Tylianakis et al. 2005). A long-term study conducted by Roubik (2001) indicates that climate is the main driver of population oscillations. He found increasing abundances of euglossine bees in years of drought (but see Tylianakis et al. 2005). In fact, total precipitation from January to October was approximately halved in 2010 compared to 2009 in our study region (VC: 686 mm in 2009 versus 347 mm in 2010, OG: 506 mm in 2009 versus 312 mm in 2010). We assume that lower precipitation in 2010 may have caused favourable conditions as for instance for the larval development of pollinators and hence, positively affected the overall insect flower visitor richness.

Our results suggest that both habitat modification and climatic variation may strongly alter insect flower visitor assemblages although we merely provide a short-term insight in the spatial and temporal pattern of insect flower visitor dynamics. Somewhat controversially, Roubik (2001) found that bee populations were rather unaffected by climatic variation over a 20-year period despite a strong inter-year variability in bee abundances. However, his study investigated the effects of climatic variability on pollinator assemblages in a relatively stable and undisturbed forest system without considering anthropogenic influences. Based on our findings, we rather assume that synergistic effects of habitat modification and climatic variability might strongly alter the prospective dynamics of animal and plant communities. This explicitly gains in importance as future scenarios predict both increasing land-use intensification (e.g., Sala et al. 2000) and a growing frequency of extreme weather conditions due to climatic change (Sala et al. 2000; Thomas et al. 2004) to foster the ongoing decline of global biodiversity.

Flower visitation

Our study demonstrates that *C. africana* is an extreme generalist tree species that is pollinated by a rather unspecialized set of pollinators. As such, this tree can be used as an appropriate model species to measure local assemblages of flower visitors across heterogeneous landscapes. Flower visitation of *C. africana* was strongly affected by forest type with increasing visitation rates in modified forests in both years. Moreover, we detected strong between-year variability in flower visitation rates. Accordingly, spatial and temporal variations of plant-pollinator interactions have been shown by numerous studies (Ricketts 2004; Tylianakis et al. 2005; Hagen and Kraemer 2010; Gomez et al. 2010). While the effects of habitat modification on the visitation rates to *C. africana* flowers were largely congruent with what we found at the insect flower visitor assemblage level, patterns of the seasonal variability were rather contradictory. Here, we recorded an increased richness of the overall insect flower visitor community in 2010, whereas the mean visitation rate observed on *C. africana* dropped by more than 60%. Thus, the dynamics of the assemblage of insect flower visitors to *C. africana* appeared to be rather uncoupled from those of the overall insect flower visitor community. This is in accordance with a study by Ricketts (2004) reporting asynchronous dynamics of different pollinator groups within the overall pollinator community. Additionally, our sampling design might have impaired these findings as we assessed the overall insect flower visitor community with traps placed at ground level whereas flower visitation to *C. africana* was observed in the canopy.

A very interesting finding of our study is that the abundance of differently sized insect flower visitors differed significantly among the forest types. Supporting our hypothesis, we found large-bodied insect flower visitors highly abundant in modified forest fragments. Conspicuously, the high flower visitation in forested gardens, secondary forests, fragments

within agriculture, and fragments within plantations was mainly due to the dominance of feral honey bees in these sites (cf. Aizen and Feinsinger 1994). Although floral abundance and plant species richness have been shown to structure pollinator assemblages (e.g., Potts et al. 2003) local flower availability did not explain the visitation rates in our study. Alternative explanations imply differences in the morphology and the physiology of differently sized pollinators. Most poikilothermal organisms conform to environmental temperatures and thus, are spatially and temporally restricted to habitats with suitable temperature conditions (Bishop and Armbruster 1999). In particular large-bodied insects show the ability to regulate and elevate their thoracic temperature due to a combination of morphological, physiological or behavioural features (Bishop and Armbruster 1999) which implies independency from local microclimate. In fact, large-bodied pollinators have been characterised by a high mobility (Steffan-Dewenter et al. 2002; Gathmann and Tscharntke 2002), which is assumed to make them less prone to habitat fragmentation and disturbance (Ricketts 2004; Schweiger et al. 2005). This would explain the assemblages of large insect flower visitors in the modified and isolated forest fragments in our study (Gathmann and Tscharntke 2002).

Specific pollinators may vary greatly in their ability to remove and transfer pollen (Alarćon 2010). These differences in the pollinator effectiveness might be caused by morphological (e.g., Stang et al. 2006), or behavioural features (e.g., Gomez et al. 2010), or by the overall pollinator abundance (e.g., Vazquez et al. 2005). In our study we could show that differently sized insect flower visitors vary significantly in their behaviour, which was independent of forest type. Intermediately sized insect flower visitors (5 – 10 mm) seemed rather effective due to the highest flower visitation frequency and a relatively long duration time per flower. Even though the largest insect flower visitors (> 10 mm) showed a significantly lower visitation frequency and shorter duration time per flower, their high abundance might compensate for these effects in the modified forests (Vazquez et al. 2005). Consequently, we assume that larger insect flower visitors (> 5 mm) had a higher effectiveness than smaller insect flower visitors. However, in the absence of pollen-load data, we cannot test this assumption.

Feral honey bees (*Apis mellifera*) are considered to be effective pollinators well adapted to fragmented landscapes (Aizen and Feinsinger 1994; Steffan-Dewenter et al. 2002). Our findings are in line with numerous studies that found a positive effect of disturbance on honey bee abundance (e.g., Aizen and Feinsinger 1994; Ricketts 2004), indicating that they might compensate for an overall loss of pollinators in disturbed habitats. However, a dependency on pollination services by only few mobile species may bear substantial risks, in particular as the last decades have shown vast breakdowns in honey bee populations (Kearns et al. 1998; Kremen et al. 2002; Ghazoul 2005). It is therefore of major importance that future conservation strategies aim to maintain a rich pollinator diversity to

secure pollination services in human modified landscapes (Kremen et al. 2002). Natural forest habitats (Ricketts 2004; Chacoff and Aizen 2006) as well as structural habitat heterogeneity (Hagen and Kraemer 2010) have been shown to act as valuable sources of pollinators, maintaining high functional diversity at a landscape scale (Gathmann and Tscharntke 2002). Although we recorded the highest insect flower visitor richness and activity in the modified forest types, natural forests may still be essential to maintain a rich regional pollinator pool.

From the pollination perspective our findings suggest that *C. africana* might benefit from habitat modification, as we detected higher flower visitation rates in the modified forests. However, the effective fruit set of *C. africana* was not affected by habitat type and the mean flower visitation rate. We assume that wind-pollination might have caused the weak relation between the effective fruit set and insect flower visitation across the different forest types, making *C. africana* at least temporary rather independent from insect pollinators. Despite the robustness of *C. africana* in respect to altered biotic pollination services, further ecological processes are involved to complete the regeneration cycle of this generalist tree species in the long term. A study from the same region indicates that seed dispersal of *C. africana* is maintained in the modified forests (Neuschulz et al. 2011). This supports the assumption that *C. africana* is relatively resistant to habitat modification. However, successful regeneration requires the availability of suitable habitat for seedling recruitment, which is likely to be limited in heterogeneous landscapes. Thus, further investigations on seedling establishment are needed to verify the long-term viability and persistence of *C. africana* in human modified landscapes.

Conclusion

In this study, we have shown that insect flower visitor assemblages and the pollination of the extremely generalist tree *C. africana* were strongly affected by both seasonality and habitat modification within a heterogeneous South African landscape. Despite strong between-year variability, overall insect flower visitor assemblages and flower visitation rates to *C. africana* trees were generally enhanced in modified forests, the latter facilitated by a high abundance of large-bodied pollinators. Consequently, our study provides encouraging results for conservation managers showing that pollination services of generalist species might be rather resilient in human modified landscapes. As an important implication for forest conservation, we emphasize that beside the protection of natural forest, the maintenance of remnant forest fragments is pivotal to sustain pollinator richness and pollination services in human modified landscapes.

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III. Effects of forest modification on bird community composition and seed removal in a heterogeneous landscape in South Africa

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Abstract

Human disturbance threatens and modifies forest ecosystems worldwide. Previous studies have investigated the effects of human impact on local bird communities in disturbed forests but we still lack information on how bird species richness and ecological processes respond to different forest modifications present at a landscape scale. In a heterogeneous South African landscape, we chose six types of indigenous scarp forest, differing in the intensity of human disturbance: continuous natural forests and natural forest fragments in nature reserves, forest fragments in eucalyptus plantations, fragments in the agricultural matrix, forest gardens and secondary forests in game reserves. In 36 study sites, we investigated the bird community using point counts and observed the seed removal of birds at the native tree species *Celtis africana*. Species richness did not differ among the forest types, but abundance varied significantly with most birds observed in fragments in the agricultural matrix, forest gardens, and secondary forests. The higher bird abundance in these forests was mainly due to forest generalists, shrubland and open country species whereas forest specialists were rarely present. Changes in species composition were also confirmed by multivariate analysis which clearly separated bird communities by forest type. Frugivore abundance in *C. africana* was highest in natural forest fragments, fragments in the agricultural matrix, forest gardens and secondary forests. The same trend was found for the estimated total number of fruits removed per *C. africana* tree, though the differences among forest types were not significant. Consequently, modified forests seem to maintain important ecological functions as they provide food sources for generalist species which may, due to their mobility, enhance natural plant regeneration. However, we could show that protected forest habitats are important refuges for specialist species sensitive to human disturbance.

Introduction

Land-use change is currently the most threatening impact on many ecosystems (Sala et al. 2000). The land cover of tropical and subtropical forests has declined dramatically over the past decades causing a vast increase of secondary forest habitats (Lewis 2006). This raises the question whether the increasing numbers of disturbed forests in human modified landscapes represent adequate habitats compensating the overall loss of natural habitats. The consequences of human disturbance on biodiversity in tropical and subtropical forest systems have intensively been studied. The results are, however, divergent for different taxa (Andrén 1994; Turner and Corlett 1996). In numerous cases, human disturbance leads to a loss of species richness (Turner 1996; Lewis 2006; Philpott et al. 2008). However, it has been reported that some species can persist in human modified landscapes to a certain degree of disturbance (Luck and Daily 2003; Peh et al. 2005) or even benefit from new habitat conditions (Ranganathan et al. 2008). Changes in species composition have been detected by studies investigating functional species groups differing in traits such as habitat preference (Farwig et al. 2009a; Farwig et al. 2009b). The way species of a certain group respond to human disturbance may strongly depend on the functional traits of species. Forest specialists, for instance, have shown to be more susceptible to human impact and thus might be replaced by generalist species in disturbed habitats (Bender et al. 1998; Peh et al. 2005; Farwig et al. 2009a). Although it remains largely unknown to which extent ecosystems are affected once the bird species of a particular functional group disappear, it has been shown for different species groups that changing species composition may substantially alter ecological functions (Larsen et al. 2005; Terborgh et al. 2008).

Birds are key players in many ecosystems and are supposed to maintain the most diverse range of ecological functions among vertebrates (Sekercioglu 2006). As important seed dispersers, they provide an essential service for natural forest regeneration (Howe and Miriti 2004; Sekercioglu 2006). Several studies suggest that forest fragmentation and disturbance might negatively affect frugivore communities and seed dispersal (Telleria and Santos 1995; Moran et al. 2004; Kirika et al. 2008a; Kirika et al. 2008b) and thus, influence the natural regeneration potential of local plant communities (Bleher and Böhning-Gaese 2001). In particular large-seeded plant species have been suggested to suffer from altered seed dispersal, depending on a small set of large-bodied vertebrate dispersers that are exposed to high hunting pressure (Forget and Jansen 2007; Terborgh et al. 2008; Holbrook and Loiselle 2009). A study of Kirika et al. (2008b) demonstrated that even small-seeded plant species are affected by disturbance. As small-seeded plant species provide food resources for a wide range of frugivores physically able to swallow the seeds, we selected the

native South African tree species *C. africana* as an adequate model species to assess the consequences of disturbance for a broad community of frugivores.

Whereas most studies from tropical forest systems showed a decrease of frugivore abundance and seed removal with increasing forest disturbance (Cordeiro and Howe 2003; Moran et al. 2004; Kirika et al. 2008b), studies conducted in agroforests showed that bird richness may be maintained at least in structurally complex habitats (Ranganathan et al. 2008; Clough et al. 2009; Maas et al. 2009). Following this rationale, it is reasonable to expect that both species richness and seed removal might decrease with increasing forest modification but may be maintained in disturbed forest habitats that sustain a certain structural complexity. Ongoing human disturbance will further turn tropical and subtropical forests into a mosaic of differently modified habitats (Gardner et al. 2009). Though frugivores have been reported to track fruit resources and pass habitat boundaries (Schleuning et al. 2011), we still lack information on how birds respond to the different forest modifications present in their home ranges. We therefore investigated the consequences of human impact on bird communities and seed removal in a complex human modified landscape in South Africa. Our study system comprised six representative types of scarp forest modification, influenced by different intensities of human disturbance, in the following referred to as different forest types.

Two main questions were addressed in the study: First, how do bird species richness, abundance and composition change in forest types of different human disturbance intensities? We hypothesized that forest specialist species are more strongly affected by human disturbance than generalists, resulting in shifts in species composition among forest types. Second, does frugivore abundance and seed removal vary among *C. africana* trees in the different forest types? Because of its small seed size, we hypothesized that *C. africana* attracts many frugivore species that maintain seed-removal services at least in structurally complex forest types.

Materials and Methods

Study area and design

Field studies were carried out from November 2008 to February 2009 in Vernon Crookes (VC) (30°16'S, 30°35'E, 2189 ha) and Oribi Gorge (OG) (30°40'S, 30°18'E, 1850 ha) Nature Reserve and the surrounding areas in the province of KwaZulu-Natal, South Africa (Fig. 1). The heterogeneous landscape to the south of Durban, strongly shaped by human land-use and urban sprawl, is covered with patches of indigenous scarp forest (von Maltitz 2003). Characterised by a remarkably rich species diversity and a high degree of endemism, these forests occur on sandstone outcrops, often in association with coastal gorges, scarps or

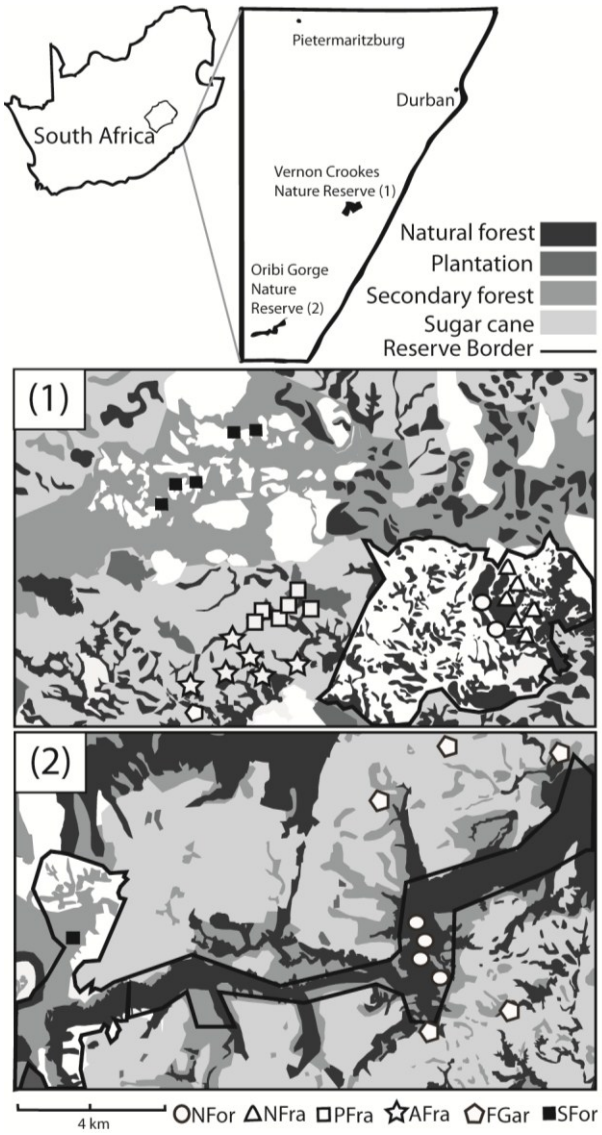

Fig. 1. Map of the study areas (1) Vernon Crookes and (2) Oribi Gorge Nature Reserve in KwaZulu-Natal, South Africa showing the location of the 36 study sites. Six sites each were located in continuous natural forests (NFor), small natural forest fragments (NFra), fragments within plantations (PFra), and fragments within agriculture (AFra), forest gardens (FGar) and secondary forests (SFor).

coastal platforms (von Maltitz 2003). Although scarp forests are naturally characterised by a patchy distribution due to microclimatic and orographic conditions (Lawes 1990), the few remnants of natural and undisturbed scarp forest are nowadays restricted to nature reserves and conservation areas. Beyond the borders of protected areas remaining forests are strongly modified by human disturbance. We selected representative types of scarp forest modification in our study region, characterised by different intensities of human impact.

As the magnitude of human impact at the landscape scale was rather complex, we desisted from ordering forest types along a disturbance gradient. Yet, dense canopy cover has steadily been suggested to be an important measure of disturbance determining a high forest species occurrence (Harvey et al. 2006; Kirika et al. 2008a; Kirika et al. 2008b). Consequently, we

used canopy cover (see 'environmental variables' section below) as a criterion for forest modification and human disturbance to classify the six representative forest types:

1) Continuous natural forests (NFor, mean canopy cover 64 % ± 10.0 SE): the largest continuous forests that were found within VC and OG Nature Reserve. The sizes of the forest blocks were 130 ha (VC) and 822 ha (OG).

2) Small natural forest fragments (NFra, 66 % ± 11.9 SE): forest islands within VC Nature Reserve formed by microclimatic and terrain conditions (mean size of the fragments: 2.3 ha ± 0.9 SE).

3) Forest fragments in timber plantations (PFra, 44 % ± 3.7 SE): small stretches of native tree species that remained within eucalyptus plantations, mostly close to river beds.

4) Forest fragments in the agricultural matrix (AFra, 34 % ± 8.0 SE): forest islands surrounded by extensive sugar cane fields, the predominant crop in the study region (mean size of the fragments: 3.2 ha ± 0.7 SE).

5) Forest gardens (FGar, 28 % ± 5.0 SE): private farm house gardens surrounded by an agricultural matrix and shaped by a mixture of old and recently planted native tree species and ornamental plants.

6) Secondary forests (SFor, 1 % ± 0.8 SE): located in private game reserves characterised by a distinct shrub cover (20 %) with predominant *Acacia* species due to decades of heavy game and cattle grazing. Due to the close vicinity to VC and OG Nature Reserve and thus, similar terrain and climate conditions, we expect scarp forest as the natural vegetation.

In total, 36 plots (50 × 50 m) were established with 6 replicates per forest type (Fig. 1). Because different forest types are not evenly distributed over the two study regions, replicate plots of most forest types are spatially clustered. However, both study regions VC and OG are located in the natural range of occurrence of scarp forests, characterised by similar soil and climate conditions as sandstone outcrops, orographic rainfall and strong winds (Cooper 1985; von Maltitz 2003). Whereas Cooper 1985 recognised both regions as coast scarp forest, a more recent study of von Maltitz 2003 assigns both reserves to two different subgroups of the scarp forest group. However, both subgroups are similar in bird species occurrence, and climate (for detailed information on forest bird species occurrence and climate data see von Maltitz 2003) as well as land-use intensity. Unambiguously, these natural environmental gradients are negligible compared to the differences among forest types caused by human modification.

Each plot contained at least one *C. africana* tree. The minimum distance between study sites was 500 m, except for the plantation sites, which were at least 200 m apart from each other. To account for the fact that there can be strong edge effects in forest fragments but not in continuous forest (Harrison and Bruna 1999), we situated all sites, including those in continuous forests, at forest gaps or edges.

Bird community

We monitored bird species richness and abundance from 10 November 2008 to 3 February 2009 within a radius of 25 m from each plot centre. Point counts (15 min) were repeated three times per study site (each once from 6 to 10 am, 10 am to 2 pm and 2 to 6 pm) over the whole observation period. To account for different weather conditions, we repeated point counts for all plots randomly over the observation period and no point counts were conducted under heavy rain. All birds that could be heard or seen were monitored by one observer (E.L. Neuschulz) to minimize observer bias. We are aware that the point count method does not provide a comprehensive evaluation of the bird community present in the study sites but rather allows a standardised comparison of bird richness among our different habitat types. We used habitat specialisation as one measure of functional diversity and classified species according to Roberts Birds of Southern Africa (Hockey et al. 2005) into either forest specialists (preferring forests and woodlands), forest generalists (preferring forest margins and sparsely wooded areas), shrubland species (preferring bush, shrub and dry open woodlands), or open country species (preferring grassland, cultivation and marshes).

Seed removal of Celtis africana

Seed removal of the native tree species *C. africana* (Ulmaceae) was investigated from 1 January to 10 February 2009 in all forest types. This common and widespread deciduous tree species is distributed from South Africa to Ethiopia and occurs in a broad range of different habitats like forests, bushveld and grassland, mostly near river margins. The fruit is a single-seeded drupe, about 6 mm in diameter and ripens from October to February. Fruits turn yellow to brownish when ripe and are distributed by a variety of frugivorous birds (Coates Palgrave 2005).

We observed each of the 36 *C. africana* trees once, starting from 6 am to 1 pm. The observations were randomly conducted over the whole observation period. All birds visiting the study trees were recorded using binoculars, observations were carried out in a distance of at least 20 m from the tree. We classified birds as either fruit consumers, seed predators or as visitors according to our observations and measured the duration time in the tree crown for every single bird. For all fruit-removing birds the number of fruits consumed per feeding time was recorded. If more than one feeding bird was present in the tree, one randomly chosen individual was selected of which fruit consumption was observed. Since there were no significant differences in the feeding activity of the four most abundant seed-removing species among the forest types, we pooled fruit consumption rates per minute for all individuals observed over all trees to calculate a mean consumption rate per minute for each species. We recorded one seed-predating species for which we used the rate of dropped non-predated fruits per minute instead of seed consumption since this better reflects its low

potential for seed dispersal. Mean consumption and fruit dropping rates respectively were then multiplied by the duration time for every bird observed in the study tree (in few cases of missing data on the duration time of a particular bird we used the mean duration time of the species pooled over all observations). Finally, products were added and averaged for all birds visiting one particular tree to estimate the total number of fruits removed per tree and the mean number of fruits removed per visit, respectively.

Environmental variables

To quantify habitat structure, we estimated canopy cover, shrub cover (vegetation 1–3 m) and open area (grassland vegetation < 1 m) with a precision of 5 % by standing in the centre of each study site. Furthermore, the diameter at breast height (dbh) of each shrub or tree > 3.2 cm was measured within a radius of 15 m around the studied *C. africana* tree to get an estimate of the age structure of the trees within the plot. We calculated mean dbh and stem density for each study site. For each study tree we recorded stem dbh, crop size and the number of fruiting trees of any species as well as overall fruit availability within a radius of 25 m around the tree.

Statistical analysis

For bird point count data, we used the species estimators Chao2, MMMean, and ICE as adequate estimators for bird species richness (Peh et al. 2005) calculated by EstimateS version 7.5.1 (Colwell 2005). Rarefied species richness accounts for the fact that species richness generally increases the more individuals are sampled (Gotelli and Colwell 2001). We tested the effect of forest type on rarefied bird species richness and bird abundance (for all species, and for forest specialists, forest generalists, open country, and shrubland species separately) using ANCOVA and ANOVA followed by Tukey's HSD multiple pairwise comparison to test for differences among the six forest types. All response variables were transformed by their natural logarithm to achieve homogeneity of variances and normality of residuals. Vegetation cover, mean dbh, and stem density were included as predictor variables with stepwise deletion of non-significant terms ($P > 0.05$).

Additive partitioning of diversity has been used to itemise the contribution of diversity components (alpha and beta) to total species diversity (gamma). This allows detecting spatial changes in species occurrence with much more precision than considering alpha diversity only (Clough et al. 2007). We partitioned the total observed bird diversity for each forest type separately and for all forest types combined as:

$$\gamma_{obs} = \alpha + \beta_1 + \beta_2$$

where α is the mean α diversity per study site, β_1 is the species turnover within sites of one forest type and β_2 the turnover among all forest types. For further details see Clough et al. (2007).

Bird community composition was also analysed using a detrended correspondence analysis (DCA) accounting for unimodal species responses. Environmental variables were post hoc fitted to the ordination plot. We tested the significance of forest types and environmental variables by random permutation (1000 iterations). Rare bird species with less than three observed individuals were excluded, so the final presence-absence matrix contained 52 bird species. Effects of forest type on frugivore abundance and total and mean seed removal of *C. africana* trees were analysed using ANCOVA and ANOVA. Crop size, mean dbh, fruit availability, and number of surrounding fruiting trees were used as predictor variables with stepwise deletion of non-significant terms ($p > 0.05$). All analyses were conducted in R (R Development Core Team 2009).

Results

Bird community

We recorded a total of 90 bird species (gamma diversity) and 1029 individuals within a total observation time of 27 h (Appendix chapter III A.1). The most abundant bird species were Dark-capped bulbul (*Pycnonotus tricolour*), Village weaver (*Ploceus cucullatus*), and Cape white-eye (*Zosterops pallidus*). Diversity estimators indicated that 54–72 % of the estimated species richness present in the study sites was recorded, with similar proportions of species detected in each forest type (Appendix chapter III A.2). There were no significant differences of rarefied bird species richness among forest types ($F_{5, 30} = 2.10$, $p = 0.094$). However, bird abundance revealed significant differences among forest types ($F_{5, 30} = 10.69$, $p < 0.001$) with most birds observed in forest gardens (back-transformed mean: 57.3 + 12.0 SE individuals), secondary forests (mean: 29.1 + 4.8 SE individuals) and fragments within agricultural matrix (mean: 27.9 + 2.8 SE individuals). High bird abundance of forest gardens and secondary forests differed significantly from all other forest types. None of the environmental variables contributed significantly to the models and thus, all variables were excluded. Functional diversity of bird communities varied significantly among the different forest types (Fig. 2, Table 1). Forest specialists were most abundant in natural forests and natural forest fragments (25 % and 13 % of all individuals recorded, respectively) and forest fragments in agricultural matrix (11 %) but very low numbers of specialists were recorded in secondary forests (2 %), forest gardens (1 %) and fragments within plantations (1 %). The latter three forest types differed significantly from the natural forests (Fig. 2). High numbers of forest generalists and shrubland species were attracted by forest gardens (65 % and 24 %, respectively) differing significantly to natural forests, natural forest fragments and fragments within plantations (Fig. 2). Most open country species were recorded in secondary forests (19 %), whereas the differences among forest types were not significant (Fig. 2).

Partitioning of diversity indicated low mean α diversity for each forest habitat (mean α over all forest types < 14 % (13 species, Fig. 3). Species turnover within forest types (β_1) varied among 21–34 % (19–31 species) in all habitat types, except for fragments within plantations, which had a low β_1 diversity of only 13 % (12 species). Forest types with lowest mean α diversity (natural forests, natural forest fragments, and fragments within plantations) strongly differed by β_1 diversity, indicating a richer overall species community within the two natural forest types than in fragments within plantations. Forest gardens shared most of their species with all other forest types (β_2 = 48 %, 47 species) whereas fragments in plantations shared only a small proportion of species (β_2 = 78 %, 20 species).

Bird communities were clearly separated in the DCA plot by forest type (R^2 = 0.66, p < 0.001, Fig. 4). The first two ordination axes explained 41 % and 33 % of the variance in species data, respectively. Forest gardens, fragments within plantations and secondary forests were clearly grouped on the left side of the plot whereas bird communities of natural forest sites, natural forest fragments and fragments within agricultural matrix were similar. According to the fitted environmental variables, sample sites were separated along the first ordination axis from left to right with increasing canopy cover. The second axis correlated with increasing dbh which is congruent with an increase of age of the trees within the study sites. All bird communities of the natural forest sites (four sites located in OG and two sites in VC) were spatially interspersed in the DCA plot, indicating that the study region had little impact on the results. Furthermore, the DCA showed similarity between all garden sites and all secondary forest sites, although one site each of the six replicates per forest type was located in the other study region.

Table 1. ANOVAs testing the effect of forest type on bird abundance grouped as forest specialists, forest generalists, shrubland- and open country species (all transformed by their natural logarithm). Given are model and error *df*-, *F*-, *p*-, and R^2- values; N = 36.

Forest type	*df*	Ln (abundance+1)		
		R^2	*F*	*p*
Forest specialists	5, 30	0.45	4.97	0.0020
Forest generalists	5, 30	0.54	7.13	0.0002
Shrubland species	5, 30	0.59	8.55	< 0.0001
Open country species	5, 30	0.39	3.80	0.0087

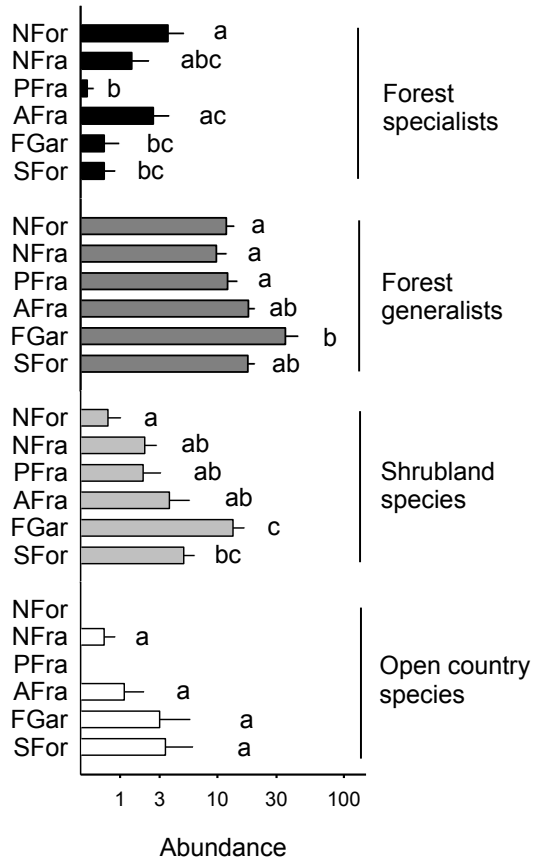

Fig. 2. Abundance of forest specialists, forest generalists, shrubland species and open country species in the six forest types: continuous natural forest (NFor), natural forest fragment (NFra), fragment within plantation (PFra), and fragment within agriculture (AFra), forest garden (FGar) and secondary forest (SFor). Shown are least square means (+ SE), different letters indicate significant differences among forest types according to Tukey's HSD multiple pairwise comparison. Note logarithmic scale for bird abundance.

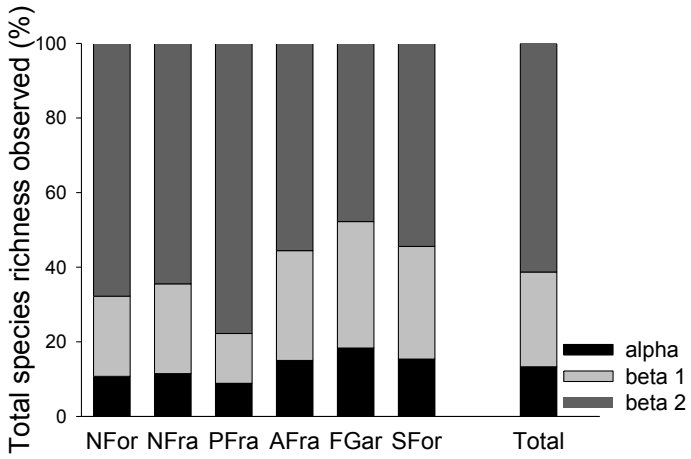

Fig. 3. Relative contribution of mean α diversity, β diversity within forest types (beta 1) and among forest types (beta 2) to overall bird species richness in the six different forest types: continuous natural forest (NFor), natural forest fragment (NFra), fragment within plantation (PFra), and fragment within agriculture (AFra), forest garden (FGar) and secondary forest (SFor).

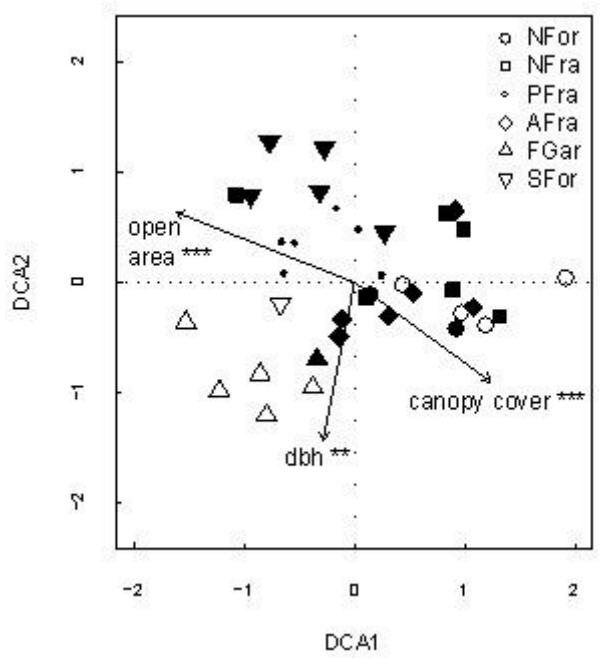

Fig. 4. DCA ordination diagram of site scores showing bird species composition in the six forest types: continuous natural forest (NFor), small natural forest fragment (NFra), fragment within plantation (PFra), and fragment within agriculture (AFra), forest garden (FGar) and secondary forest (SFor). Fitted environmental variables were canopy cover, open area and mean dbh of trees within the study sites (*** $p < 0.001$, ** $p < 0.01$). Filled symbols represent study sites in the Vernon Crookes region, open symbols represent sites in the Oribi Gorge region. First and second axis explained 41 and 33 %, respectively.

Seed removal of Celtis africana

Out of 64 bird species recorded in all study trees within a total observation time of 252 h, we observed 15 fruit consuming species (23 %). We detected one seed-predating species, the Thick-billed weaver (*Amblyospiza albifrons*), which we assumed to contribute only little to successful seed dispersal (> 98.5 % seed predation observed). Despite its high seed-predation rate, we regarded this species as dispersing species since it contributed to seed dispersal by dropping non-predated fruits. Visitation rates of the Thick-billed weaver accounted for 25 % of all fruit consuming birds in secondary forests but they were less abundant in forest gardens (12 %), fragments within agricultural matrix (13 %) and natural forests (15 %). There was negligible to no seed predation in natural forest fragments and fragments within plantations.

The abundance of fruit-eating birds in *C. africana* trees varied significantly among the different forest type ($F_{5, 30} = 2.95$, $p = 0.028$, Fig. 5 a). Most fruit-removing birds in *C. africana* trees were recorded in secondary forests (back-transformed mean: 8.1 + 3.4 SE individuals), forest gardens (mean: 6.4 + 4.6 SE individuals), forest fragments in agricultural matrix (mean: 5.6 + 3.3 SE individuals), and natural forest fragments (mean: 3.4 + 2.8 SE individuals). Low numbers were recorded in natural forests (mean: 2.9 + 0.9 SE individuals)

and fragments within plantations (mean: 0.6 + 0.4 SE individuals), whereas only the latter differed significantly from secondary forests (Fig. 5 a). We found no significant effect of the environmental variables and thus excluded them from all further models. Seed removal did not differ among forest types ($F_{5, 30} = 1.95$, $p = 0.115$, 5 b), even though we estimated higher total fruit removal rates in natural forest fragments, forest fragments in agricultural matrix, forest gardens, and secondary forests than in natural forests and fragments within plantations. High removal rates were mainly based on higher visitation rates by birds, since mean removal rates per visiting bird did not vary among the forest types ($F_{5, 30} = 0.27$, $p = 0.927$).

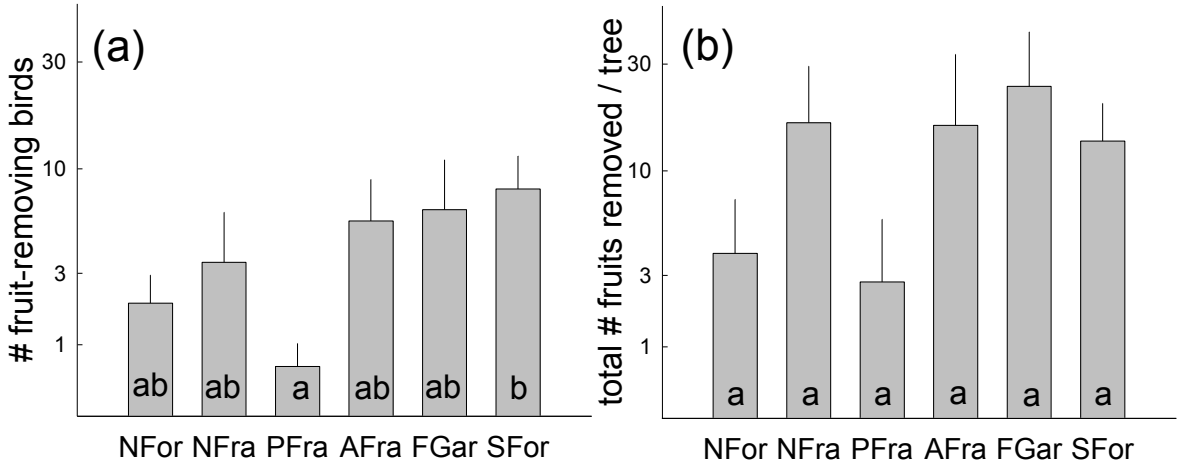

Fig. 5. (a) Abundance of fruit-removing birds recorded in *C. africana* during 7 h, and (b) estimated total number of fruits removed per tree, compared among the six different forest types: continuous natural forest (NFor), natural forest fragment (NFra), fragment within plantation (PFra), and fragment within agriculture (AFra), forest garden (FGar) and secondary forest (SFor). Shown are least square means (+ SE), different letters indicate significant differences among forest types according to Tukey's HSD multiple pairwise comparison. Note logarithmic scale for the abundance of fruit-removing birds and the estimated total number of fruits removed per tree.

Discussion

Bird community

Bird species richness was not significantly affected by human disturbance. However, we detected significant variation in bird abundance and species composition among the six forest types. Compositional changes have been suggested to negatively affect ecological functions (Terborgh et al. 2008). Based on a global data base of bird species, Tscharntke et al. (2008) could show strong shifts in avian functional diversity regarding species' diet in tropical forest communities compared to tropical agro-forests and agricultural systems. In a study by Farwig et al. (2009a) bird functional groups changed along forest habitats in such way that forest specialists strongly declined with increasing forest modification. The same was observed in our study system where forest generalists, shrubland and open country

species became more abundant with increasing forest modification, whereas forest specialists strongly declined in these forest types. This may be exemplified by the comparison of two species, the Dark-backed weaver (*Ploceus bicolour*, forest specialist) and the Black-headed oriole (*Oriolus larvatus*, forest generalist), both likewise abundant in natural continuous forests (in total nine and eight individuals, respectively). While the Dark-backed weavers declined in intensely modified forest sites (one individual recorded in secondary forests, no individuals in forest gardens and plantations), the numbers of Black-headed orioles remained largely constant (six individuals recorded in plantations, seven in secondary forests and eight in forest gardens). This clarifies that even though some species are able to persist, particularly specialised species as the Dark-backed weaver are among the first that disappear in modified habitats (Ranganathan et al. 2008; Tscharntke et al. 2008). Ordination analysis of the bird community verified that species composition strongly changed with altered environmental conditions. Local environmental gradients among the two study regions and the local clustering of most replicates per forest type were negligible compared to the effects of habitat modification on bird communities. The bird community of undisturbed forests, comprising a high proportion of specialist species, was clearly linked with high canopy cover and an intermediate dbh, as the forests consisted of old tree stems as well as younger undergrowth trees. In contrast, the bird community of secondary forests, mainly composed of generalist species, did not depend on high canopy cover and miscellaneous tree ages supporting the assumption that generalists are more robust to habitat modification. Thus, bird species composition was strongly affected by forest type demonstrating that habitat modification on a relatively small spatial scale can have decisive effects on bird communities.

In contrast to previous studies from tropical forest systems, we recorded more birds in most human modified sites than in natural forests or natural forest fragments (Peh et al. 2005; Farwig et al. 2006; Kirika et al. 2008b). Yet, studies conducted in tropical agro-forest systems suggested that bird richness may be maintained or even enriched in disturbed but structurally complex forest habitats (Estrada et al. 1993; Ranganathan et al. 2008; Clough et al. 2009; Farwig et al. 2009a). The forest surrounding matrix might compensate for disturbance induced species loss in attracting generalist species that benefit from resource availability and connectivity (Brotons et al. 2003), whereupon the mobility of birds may foster these compensatory effects. Movement pattern among forest fragments however are suggested to be determined by the quality of the matrix (Turner 1996). Low mean α and β_1 diversity in fragments within plantations indicated that these sites were occupied by a species poor bird community. We assume that the surrounding matrix of dense eucalyptus trees may contribute to hinder the location of native forest fragments within plantations and thus, explain the low attractiveness of this forest type to most bird species.

Comparing forests of different disturbance intensities at a landscape scale enabled us to demonstrate the contribution of modified forests to maintain bird species richness in

human disturbed landscapes. Altered forest habitats as for instance forest gardens, fragments within agricultural matrix or secondary forests in our study system may represent valuable stepping stones for many bird species (Sekercioglu et al. 2007) indicating a high conservation value. The bird community of fragments within plantations, however, was strongly affected by forest modification demonstrating a high degree of disturbance. Furthermore, the loss of specialist species in modified forests demands that great conservation effort needs to be focused on species sensitive to habitat changes and disturbance (Luck and Daily 2003). In particular shifts in species' abundance, composition and functional diversity are good indicators for detecting the effects of human disturbance on ecosystems.

Seed removal

We observed more frugivorous birds visiting *C. africana* trees in natural forest fragments, forest fragments in agricultural matrix, forest gardens, and secondary forests than in natural continuous forests and fragments within plantations, whereas visitation rates only differed significantly between secondary forests and fragments within plantations (Fig. 5 a). This general pattern was congruent with the overall bird abundances detected in the different forest types. High visitation rates by frugivorous birds in fragmented or disturbed forests have been described for several tropical tree species (e.g., Luck and Daily 2003; Farwig et al. 2006; but see Cordeiro and Howe 2003). Although a number of 15 fruit-removing bird species recorded in the *C. africana* trees appeared to be relatively low, our results are in line with other studies conducted in the same study region showing similar or even smaller feeding guilds (Bleher and Böhning-Gaese 2001; Voigt et al. 2011). Interestingly, estimated mean fruit removal rate of all birds per tree was equal in all forest types in our study area. Thus, a high total removal rate of a particular tree was based on a high abundance of fruit consuming birds and not on differences in species' feeding behaviour and species composition (Fig. 5b). In fact, it is suggested by Vazquez et al. (2005) that it is species' abundance that determines effective seed removal rather than specific differences in fruit removal rates.

There are several explanations for high visitor abundance and thus high total fruit removal in modified forest sites compared to relatively low visitor abundance in natural forests and forest fragments within plantations. In human disturbed landscapes, a concentration of mobile organisms within suitable forest fragments has been reported (Lovejoy et al. 1986; Bowman et al. 2002) resulting from limited habitat availability but also from a certain habitat attractiveness including for instance shelter, nesting sites, and food resources for many species. However, our results showed that crop size and local fruit availability had no significant effect on either bird visitation rates or on total fruit removal, which also has been reported in previous studies (Kirika et al. 2008b; Lefevre and Rodd 2009). As suggested by Thompson and Willson (1978), it is not higher fruit availability, but

rather higher perceptibility of fruit resources that attracts more fruit consuming birds in disturbed sites, like forest edges or gaps. However, in the natural continuous forest, we selected our study trees not in the interior forest but close to forest gaps or edges where perceptibility should have been comparable. As sampling effort is usually limited in field surveys, we assessed fruit availability only locally, on a scale of 25 m around the study tree. Since continuous forests comprised more total area, overall availability of fruiting trees could have been higher on the larger spatial scale (Farwig et al. 2006), which might have caused a dispersion of fruit-consuming birds and thus, might have reduced fruit removal rates per tree.

From the plants' perspective, dispersing seeds is crucial for successful regeneration and in the long term for species' persistence. Mobile organisms like birds show the ability to disperse seeds over long distances (e.g., Holbrook and Smith 2000) and are moreover able to significantly increase seed rain in disturbed areas (Au et al. 2006). We conclude from our findings that *C. africana* is potentially able to regenerate in modified forests due to guaranteed seed dispersal. The recruitment of animal dispersed tree species may benefit from the mobility of birds connecting different forest types at the landscape scale and at the same time modified forest types represent important food sources for many generalist bird species. However, regeneration processes depend on the availability of suitable habitat for seedling establishment, which might be limited in heterogeneous landscapes. Following seed dispersal, seedling establishment requires an appropriate interaction of abiotic and biotic factors and whether or not natural recruitment is increased in these human modified forest types needs to be investigated.

Conclusions

We showed in our study that forest modification significantly affected overall bird community and abundance of frugivorous birds visiting the native tree species *C. africana* in a heterogeneous South African landscape. Our findings demonstrate that many generalist bird species may persist in disturbed forests compensating the loss of specialist species and thus, enhancing bird abundance and maintaining seed removal. Consequently, substitute forest habitats and forest remnants may contribute to support bird richness and natural recruitment processes in heterogeneous landscapes. However, this might not apply for all forms of forest modification, as in our study the forest fragments within plantations were low in bird abundance. Furthermore, some species as for instance forest specialists may suffer more from habitat modification than generalist species. We recorded enriched bird abundance in most modified forest types, but at the same time our results indicate the importance of protected forest habitats acting as refuges for bird species sensitive to human disturbance.

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IV. Frequent bird movement activity across a highly fragmented landscape: the role of species traits and forest configuration

With Mark Brown and Nina Farwig (*Submitted*)

Abstract

Previous studies that tracked the movements of single bird species within human modified landscapes have shown contradictory results on the ability of forest birds to disperse across matrix habitat. Functional guild specificity as well as landscape characteristics have been shown to determine bird movement activity, but the responses may largely differ among species of a community. Thus, studies investigating how these factors influence the movements of entire bird assemblages across fragmented landscapes are essential but have hardly been conducted until now. In this study, we determined how species traits and forest configuration shape bird movements among nine differently modified forest patches in a highly fragmented South African landscape. We combined 90 hours of bird observations with capture-mark-recaptures (104754 mist-net hours) to distinguish between movements among patches (all birds that conduct long-distance movements across the landscape) and movements within patches (all resident birds that conduct only short-distance movements within a fragment). Overall, we detected a high movement activity of forest birds across the fragmented landscape. Dietary specialization, habitat affinity and body mass strongly shaped the relative dispersal of bird species across the nine fragments with frugivorous birds, forest specialists and large-bodied species showing the highest dispersal abilities. In contrast, resident insectivores and forest generalists tended to move only within particular forest fragments. Our results suggest that remnant forest fragments may represent valuable stepping-stones as well as permanent habitat for local bird assemblages. We emphasize that beside the conservation of natural forests, the maintenance of structurally rich forest fragments that create connectivity due to close vicinity to each other is pivotal to maintain regional forest bird assemblages in human-modified landscapes.

Introduction

Land-use and agricultural intensification have caused an unprecedented decline of global forest cover (Lewis 2006) that led to a loss of biodiversity in fragmented landscapes (Turner 1996; Fahrig 2003). The impact of forest fragmentation on species communities varies immensely among taxonomic groups (Turner 1996). Birds, as highly mobile species, are considered to be less affected by fragmentation than other taxonomic groups of lower mobility (Harris and Reed 2002; Price 2006; Lees and Peres 2009; Marini 2010). In contrast, several long-term studies have shown that forest fragmentation can severely affect the persistence of bird assemblages (Stouffer et al. 2006; Ferraz et al. 2007; Lees and Peres 2009).

Less obvious than alterations in species diversity are behavioural changes of birds caused by fragmentation. Notwithstanding, changes in bird movement behaviour may profoundly affect ecosystem functionality. Migratory frugivores, for instance, conduct shorter movements in fragmented than in continuous forests, despite their ability to overcome large distances (Price 2006). Such altered movements have severe consequences for fleshy-fruited plants as frugivorous birds represent important seed dispersing vectors and thus link local plant populations (Bleher and Böhning-Gaese 2001).

How birds move through disturbed landscapes may depend on a large range of different factors (Knowlton and Graham 2010). Guild-specific responses have widely been described to shape bird movement activities in heterogeneous landscapes (e.g., Harris and Reed 2002; Laurance et al. 2004; Lees and Peres 2008; Gillies and St Clair 2010). Species traits, such as body size, dietary or habitat specialization are related to movement activities and thus may well predict bird dispersal across a landscape. Large-sized frugivores, for example, exhibit physiological capabilities to cross open habitat while foraging for food (Spiegel and Nathan 2007) and therefore have been suggested to be less prone to forest fragmentation (Lees and Peres 2008). In contrast, small and less mobile forest specialists have shown a strong sensitivity towards disturbance (e.g., Harris and Reed 2002). Consequently, local bird assemblages comprise highly mobile bird guilds that move among the landscape as well as less mobile species that conduct short-ranging movements within the understorey of a fragment. Additionally, landscape characteristics, such as the degree of isolation, patch connectivity and matrix type, have been shown to determine bird movements across heterogeneous landscapes (Graham and Blake 2001; Price 2006; Kennedy et al. 2010). Moreover, habitat quality such as fragment size and structure may decisively influence bird movements (Stouffer and Bierregaard 1995; Zanette et al. 2000; Graham and Blake 2001). While small and structurally homogeneous patches might be actively avoided, large and heterogeneous forest fragments may attract birds in search of food, nesting habitat or shelter.

Although numerous previous studies have radio tagged or dislocated single bird species to follow up their individual movements (e.g., Graham 2001; Sekercioglu et al. 2007; Hansbauer et al. 2008; Robertson and Radford 2009; Hansbauer et al. 2010; Gillies and St Clair 2010; Lenz et al. 2011), extensive community-based studies are scarce and, to our knowledge, limited to fragmented forest landscapes in Brazil (Laurance et al. 2004; Lees and Peres 2009; Marini 2010). Yet, understanding bird responses at a community level is of great importance as ongoing habitat fragmentation globally threatens the landscapes of the present days. Here, we present the first study from Africa that investigates how functional traits and forest configuration shape the movements of an entire bird assemblage in a highly fragmented landscape. We combined bird observations with capture-mark-recaptures to distinguish between 1) movements among patches including all species that conduct large-ranging movements across forest fragments and 2) movements within patches that are all "resident" birds of a fragment, which we assume to conduct only short-ranging movements within the respective patch. We asked whether functional traits predict bird community movements among and within forest patches and how both large- and short-ranging movements are affected by forest fragment configuration. To address these questions, we applied a novel version of the fourth-corner analysis (Dray and Legendre 2008) linking species traits (dietary specialization, habitat affinity and body mass) to habitat variables (forest type, human disturbance, fragment size, and canopy cover). We hypothesized that large-sized and generalist species easily cross modified landscapes in search for food sources. In contrast, we expected that small-sized and specialist species remain in remnant forest fragments due to their sensitivity toward habitat modification.

Methods

Study area

We conducted our study within and around Vernon Crookes (VC) Nature Reserve (30°16'S, 30°35'E, 2189 ha) in KwaZulu-Natal, South Africa. The natural vegetation of the region is characterised by grassland and scattered patches of indigenous scarp forest (Cooper 1985). Today, only a few undisturbed scarp forests persist in conservation areas, but numerous fragments remain in human-modified landscapes. Such privately owned patches have been shown to be important for forest bird conservation in South Africa (Brown 2006). We investigated the bird communities of nine forest fragments characterized by different configuration and surrounding matrices: 1) Natural forest fragments within VC Nature Reserve (NFra, 2.3 ha ± 1.5 SD). These undisturbed forest patches occur naturally due to microclimatic and terrain conditions and are surrounded by natural grassland. 2) Forest fragments embedded in a matrix of sugar cane fields (AFra, 4.7 ha ± 0.7 SD) at the border of VC Nature Reserve. 3) Forested farm gardens (FGar, 1.4 ha ± 0.5 SD). These sites are shaped

by a mixture of native and recently planted ornamental plants and are also surrounded by sugar cane fields. We estimated canopy cover with a precision of 5% by standing in the centre of each fragment. The size of each fragment was recorded using a Global Positioning System (range of all fragments: 0.5–5.4 ha, mean = 2.8 ha ± 1.7 SD). The smallest distance between the study sites was 0.5 km, the largest distance 10 km (mean = 5.5 km; Fig. 1).

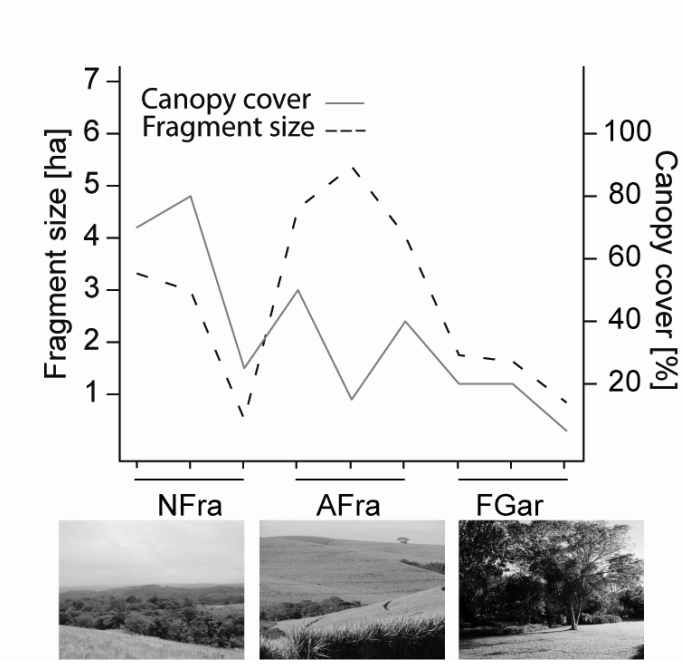

Fig. 1 Fragment size [ha], and canopy cover [%] of the nine study sites. Non-forest matrix is grassland within VC Nature Reserve, and sugar cane outside the reserve borders. NFra = natural forest fragment, AFra = fragment within agriculture, FGar = forested garden.

Among-patch community

We observed bird movements from Sep to Nov 2010 at times of high bird activity from 5:00 to 10:00 am and from 15:00 to 17:00 pm. Each of the nine study sites was observed on seven to ten occasions, resulting in a total of ten observation hours per fragment (eight hours in the morning and two hours in the afternoon, respectively). Observations were conducted standing in a distance of 50 to 80 m from the border of each fragment. The position of the observer (E.L. Neuschulz) was variegated at each observation day to avoid sampling effects and unsuitable light conditions. We identified all birds flying into or out of the fragments using binoculars. Individual birds entering and leaving the fragment within one observation session were only counted as one movement event in the analysis. Thus, we defined the among-patch community as all birds that were observed flying to or from one of the nine forest fragments. We classified all species into functional guilds according to their diet (frugivore, insectivore, omnivore, nectarivore, granivore and carnivore) as described in Hockey et al. (2005). Moreover, the habitat affinity of a species was categorized according to Hockey et al. (2005) and Oatley (1989) as forest specialist (preferring forests and

woodlands), forest generalist (preferring forest margins and sparsely wooded areas), shrubland species (preferring bush, shrub and dry open woodlands), or open-country species (preferring grassland, cultivation and marshes). We classified the body mass of the species according to Hockey et al. (2005) and based on own measurements (see below).

Within-patch community

We captured and recaptured birds using mist-nets from Oct to Nov 2010 and from Feb to Mar 2011. At each site we trapped birds thrice in 2010 and twice in 2011 for 1.5 days each with a minimum of seven days between consecutive trapping events, resulting in a total of 7.5 trapping days per site. Mist-nets were opened at dawn and left open until dusk at the first and until midday at the second trapping day, respectively. On average we conducted 11,639 ± 966 SE mist-net hours per forest fragment over the whole study period (total over all sites: 104,754 mist-net hours). One mist-net hour represents one 12 m net open for one hour. We defined all birds that were caught at least twice in different trapping events as recaptures. Birds that were caught a second time at the same or the following trapping day were not considered as recaptures. We separated the recaptured birds that dispersed from their original ringing site from those that were caught at the same site. Finally, we defined the within-patch community as those birds that were recaptured at least once at their original ringing site and, additionally, that were not observed during among-patch movements. All captured birds were described, marked with uniquely numbered leg bands, and measured before releasing them at the catching site. As body mass was highly correlated with measurements related to bird mobility (e.g., body size or wing length) we excluded these variables from further analyses.

Data analyses

To allow an in-depth comparison of the species richness of both among- and within-patch communities, we used additive partitioning to itemise the contribution of diversity components (α and β) to total species diversity (γ). We partitioned the total observed diversity of both communities according to Clough et al. (2007) as:

$\gamma_{obs} = \alpha + \beta1 + \beta2$ where α is the mean α diversity per fragment, β1 is the species turnover within the sites of one forest type and β2 the turnover among all forest types.

We then analysed how species traits shaped the movements of both among- and within-patch communities. In a first step, we estimated the relative dispersal of different functional guilds (classified according to their diet, habitat affinity and body mass) across the nine fragments based on the observed among-patch movements. We used an index developed by Tylianakis et al. (2005), which compares observed and expected numbers of each species in each of the nine sites regardless of forest type. The expected number of individuals of a species *i* within a plot *j* is given by $E_{ij} = N_i \times P_j$, with N_i representing the total number of

individuals of species *i* in all fragments and P_j as the proportion of all species sampled (in all fragments) that was found in plot *j*. By using $\log_{10}([O_{ij} / E_{ij}] + 1)$ with O_{ij} as the observed number of individuals of species *i* in plot *j*, we calculated the relative dispersal for each species *i* in each plot *j*. Given this formula, we obtained an even dispersal of species *i* within all sites at an index value of 0.3. Deviations from an index value of 0.3 indicate the preference of a species to particular fragments.

In a second step, we used a novel version of the fourth-corner analysis to directly measure the link between species traits and environmental data (Dray and Legendre 2008). In the fourth-corner procedure, a matrix **L** with species abundances is related to a matrix **R** with variables describing the environmental conditions of the sites and a matrix **Q** describing various species traits.

Our first objective was to assess how species traits and habitat variables shape among-patch bird communities. Thus, the species matrix ($\mathbf{L_{A\text{-}P\text{-}C}}$) contained all species that were recorded during the movement observations. To reduce the influence of differences among absolute abundances recorded in the different forest types, Hellinger transformation was applied (Legendre and Gallagher 2001). The environmental matrix (**R**) contained the three fragment types (NFra, AFra, FGar) coded 0 or 1. A variable "human disturbance" separated the natural fragments (coded as 0) form fragments within agriculture and forested gardens (coded as 1). Two continuous variables, fragment size and canopy cover, were included into the matrix. To test whether trapping effort had an effect on functional guilds, we included the number of mist-net hours in the analysis of the within-patch community. The trait matrix (**Q**) constituted of three species traits: dietary specialization, habitat affinity, and body mass as a quantitative variable. We used the permutation model 1 (9999 permutations), (Dray and Legendre 2008), which permutes all species within an entire column of the **L** matrix to test the null hypotheses of randomly dispersed across sites. This model corresponds best to our data as we assume birds to freely disperse throughout the landscape due to their mobility. The alternative hypothesis states that species are dispersed according to their environmental preference.

Our second objective was to compare the results of fourth-corner analysis of the among-patch communities to a subsequent analysis linking species traits, habitat variables and within-patch bird communities. Thus, we repeated the analysis with a second matrix ($\mathbf{L_{W\text{-}P\text{-}C}}$) of the within-patch community that contained abundance data of all "resident" birds. All fourth-corner analyses were performed using the function "fourthcorner" of the ade4 package (Dray and Dufour 2007) in the R language (R Development Core Team 2010).

Results

Community analysis

Within a total of 90 hours observation time we recorded 3,908 movements of 55 bird species to and from the nine fragments representing the among-patch community (Fig. 2a, Appendix chapter IV A.1). Furthermore, we captured a total of 1,454 birds belonging to 104 species by mist-netting. Out of these, 50 species were also observed to conduct among-patch movements. The recapture rate was 15% (215 individuals, 45 species). While 12 species (19 individuals) of the recaptures dispersed from their original ringing site, 41 species (196 individuals) were recaptured at their original catching site (Fig. 2b, Appendix chapter IV A.1). Out of these, 20 species (93 individuals) were not observed during among-patch movements and thus were defined as the within-patch bird community. We excluded two species, Little and White-rumped swift, as they appeared as "resident birds" in forested gardens due to breeding activities, though we assume their foraging ranges to outreach the respective fragment.

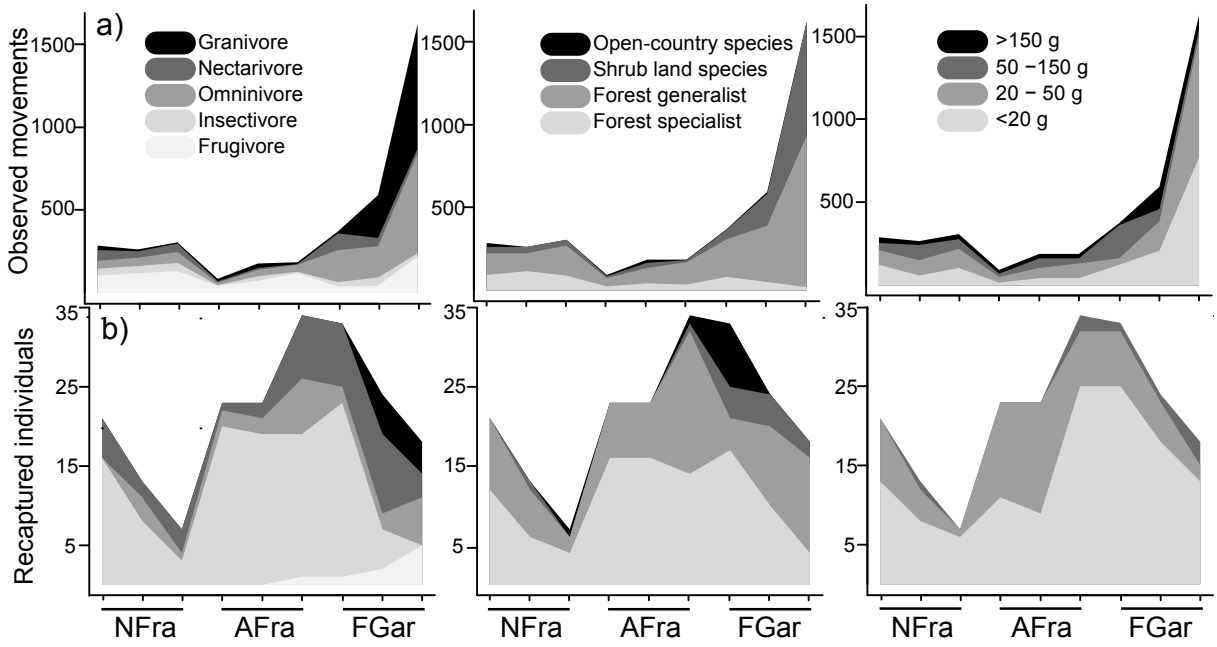

Fig. 2 Observed movement activities (a) and number of recaptured birds (b) in the nine study sites. Birds are classified according to their dietary specialization, habitat affinity and body mass. NFra = natural forest fragment, AFra = fragment within agriculture, FGar = forested garden. Note different scaling of y-axes.

Diversity partitioning revealed a high mean α diversity over all nine fragments for the among-patch community (28 species, 50%). The species turnover within the various forest types (β_1 = 30%, 16 species) was much higher than the turnover among the forest types (β_2 = 20%, 11 species). In contrast, we found very low mean α diversity for the within-patch

community (5 species, 26%). While the turnover within the various forest types was similar compared to the among-patch community (β1 = 28%, 5 species), species turnover among the forest types was much higher (β2 = 46%, 8 species).

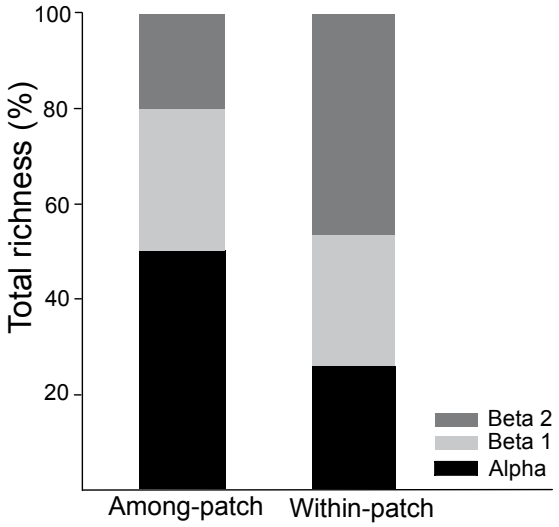

Fig. 3 Percentage of total bird species richness explained by alpha and beta components of diversity after additive partitioning of the among- and within-patch communities. Alpha = mean number of species within all forest fragments, beta 1 = species turnover within a specific forest type, beta 2 = species turnover among the three forest types.

Response of functional guilds to habitat modification

The among-patch community was significantly structured by functional traits. We found that frugivorous birds evenly dispersed across the nine fragments (Fig. 4). Moreover, the relative dispersal of nectarivores approximated evenness across fragments, whereas among-patch movements of insectivorous, omnivorous and granivorous birds deviated from an even dispersion due to prevalent abundances in specific fragments. Surprisingly, among-patch movements of forest specialists were relatively even across fragments, whereas the dispersal of generalist, open-country and shrubland species was erratic across fragments (Fig. 4). Though abundance of large-bodied species was low, they were rather evenly dispersed across fragments, whereas abundances of species lighter than 150 g diverged from an even dispersion (Fig. 4).

We recorded an anecdotal number of 19 individuals by mist-netting dispersing from their original ringing site and thus could be considered as part of the among-patch community (Appendix chapter VI A.1). However, as individual among-patch movements were scarce, we refrained from further analyses.

Based on the fourth-corner analysis, we found significant relationships among various functional traits and environmental parameters in the among-patch community (Table 1). High movement activity of frugivores was strongly associated with natural fragments as well as fragments within agriculture. Furthermore, frugivore movements were positively

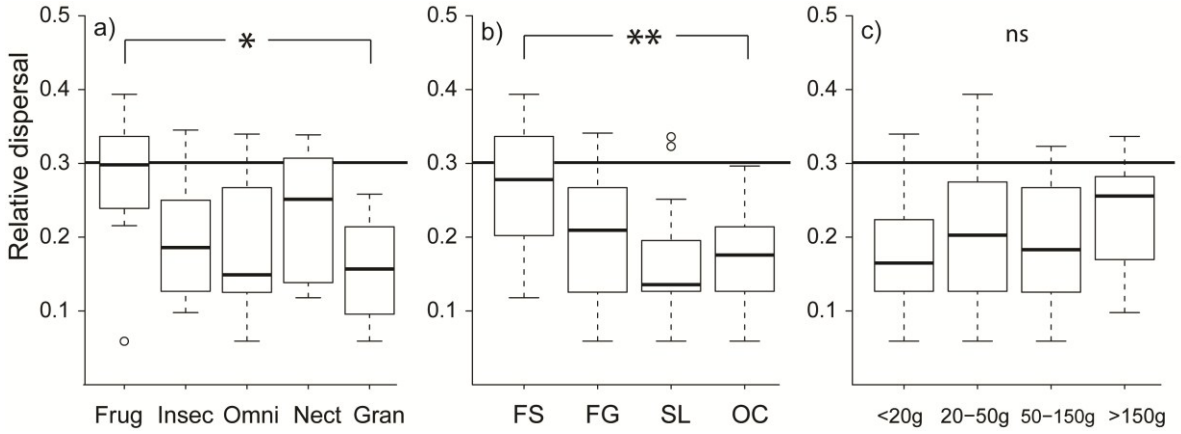

Fig. 4 Relative dispersal of bird guilds among the nine forest fragments based on an index modified from Tylianakis *et al.* (2005). Functional groups are classified according to (a) dietary specialisation (Frug = frugivore, Insec = insectivore, Omni = omnivore, Nect = nectarivore, Gran = granivore), (b) habitat affinity (FS = forest specialist, FG = forest generalist, SL = shrubland species, OC = open-country species), and (c) body mass. Black line at a relative dispersal of 0.3 indicates an even dispersion across all nine forest fragments. Brackets show significant differences (*$p < 0.05$, **$p < 0.01$, ns = not significant)

correlated to fragment size and canopy cover. Granivorous species were also positively associated with natural fragments but movement activity decreased with increasing canopy cover. In contrast, the movement activity of insectivorous species had a strong positive association with agricultural fragments, forested gardens and thus, human disturbance. The movement activity of forest specialists increased significantly with increasing canopy cover and was highest in natural fragments. We found a positive association between open-country species and fragment size. While large-sized birds were positively associated with fragments within agriculture and large fragment size, higher movement activities of small-sized birds were linked to forested gardens (Table 1).

Fourth-corner analysis of the within-patch community revealed that insectivores were strongly associated with fragments within agriculture and forested gardens (Table 2). Forest generalists and open-country species were positively correlated to fragments within agriculture. We found no significant relation among any species traits and the overall mist-net hours per site, indicating that slight differences in the mist-net hours among the different sites did not affect the sampling.

Table 1 Fourth-corner analysis of the among-patch movements related to species traits and environmental variables. Given are significant positive [+] or negative [–] relationships after Pearson correlation. Single signs represent significance level of $p < 0.05$, double signs $p < 0.01$, and triple signs $p < 0.001$, marginal significant correlations $p < 0.1$ given in brackets. Circle: non-significant relationship. NFra = natural forest fragment, AFra = fragment within agriculture, FGar = forested garden, frug = frugivore, insec = insectivore, omni = omnivore, nect = nectarivore, gran = granivore, FS = forest specialist, FG = forests generalist, SL = shrubland species, OC = open-country species.

Traits		NFra	AFra	FGar	Human disturbance	Fragment size	Canopy cover
Diet	frug	++	+	∘	∘	+	+
	insec	∘	++	+	++	∘	∘
	omni	∘	∘	(+)	∘	∘	∘
	nect	∘	∘	∘	∘	∘	∘
	gran	+	∘	∘	∘	∘	– –
Habitat	FS	+	∘	∘	∘	(+)	++
	FG	∘	∘	∘	∘	∘	∘
	SL	∘	(+)	∘	∘	(–)	(–)
	OC	∘	∘	∘	∘	+	∘
Mass		∘	+	–	∘	+	∘

Table 2 Fourth-corner analysis of the within-patch bird communities related to species traits and environmental variables. Given are significant positive [+] or negative [–] relationships after Pearson correlation. Single signs represent significance level of $p < 0.05$, double signs $p < 0.01$, and triple signs $p < 0.001$, marginal significant correlations $p < 0.1$ given in brackets. Circle: non-significant relationship. NFra = natural forest fragment, AFra = fragment within agriculture, FGar = forested garden, insec = insectivore, omni = omnivore, FS = forest specialist, FG = forests generalist, SL = shrubland species, OC = open-country species.

Traits		NFra	AFra	FGar	Human disturbance	Fragment size	Canopy cover	mist-net hours
Diet	insec	(+)	+++	+	(+)	∘	∘	∘
	omni	∘	∘	∘	∘	∘	∘	∘
Habitat	FS	(+)	(+)	∘	∘	(–)	∘	∘
	FG	∘	+	(+)	∘	∘	∘	∘
	SL	∘	∘	∘	∘	∘	∘	∘
	OC	∘	+	∘	∘	∘	∘	∘
Mass		∘	∘	∘	∘	∘	∘	∘

Discussion

Community analysis

Our results show that the movement behaviour of an entire bird assemblage within a heterogeneous landscape is strongly affected by both species' functional traits and fragment configuration. Overall, we recorded a high α diversity of among-patch communities, indicating that various birds move through the landscape using natural forest fragments within nature reserves, as well as patches surrounded by agricultural matrix and forested gardens. This is in line with previous studies showing high flexibility of selected forest birds (Price 2006; Hansbauer et al. 2010; Marini 2010; Lenz et al. 2011) and the ability of entire bird assemblages to disperse in fragmented landscapes (Lees and Peres 2009; Marini 2010; Gillies et al. 2011). In contrast, mean α diversity was low within the patches, indicating that only few species persisted in the fragments. These findings imply low resource availability for populations within the fragments. Furthermore, species turnover among the different forest types (β2 diversity) was remarkably high for the within-patch community. This suggests that habitat modification severely affected within-patch communities leading to strong compositional changes across the forest types.

Response of functional guilds to habitat modification

Even though most birds showed a general ability to move among patches, we found significant differences in the movement activity among functional guilds. In particular, frugivorous and nectarivorous birds, forest specialists and large-bodied species showed the highest dispersal abilities (Fig. 2).

Food resource availability has been shown to strongly shape bird movements across heterogeneous landscapes (Kennedy 2010, Zanette et al. 2000, Graham 2001). Frugivores or nectarivores, for instance, are functional guilds which depend on food sources that occur highly clustered in fragmented forests and furthermore, are determined by high seasonal variability. They are obliged to track their food plants over large distances across the landscape (Graham 2001; Berens et al. 2008; Schleuning et al. 2011) and thus may show little response to habitat modification. In spite of the good overall dispersal abilities of frugivores in the study area, we found a significant positive association among frugivores and natural, as well as agricultural fragments, fragment size and canopy cover. Large fragments seemed to comprise more fruits compared to small patches (Da Silva and Tabarelli 2000) explaining the strong response of frugivore abundances to fragment size (Stouffer *et al.*, 2006). Food availability is also a decisive factor explaining low performance of insectivores in small fragments (Zanette et al. 2000; but see Sekercioglu et al. 2002). In fact, numerous previous studies have shown a decline of insectivorous birds in fragmented landscapes (Stouffer and Bierregaard 1995; Sekercioglu et al. 2002; Stouffer et al. 2006). Our study contrasts these

findings showing a strong positive correlation between insectivore movement activity and human disturbance. This might be explained by the relatively high insect richness within forest gardens and agricultural fragments within this study area (E.L. Neuschulz et al., *submitted.*). A spill-over of insects from the agricultural matrix into agricultural forest fragments and forested gardens might have increased insect availability (Tscharntke et al. 2005) and thus fostered the close association between insectivores and human disturbance.

Interestingly our study showed that forest specialists dispersed almost evenly across fragments (Fig. 4). These findings seem contradictory to numerous previous studies showing high sensitivity of specialist species in disturbed landscapes (e.g., Farwig et al. 2009; Clavel et al. 2011; Neuschulz et al. 2011). Yet, the fourth-corner analysis revealed that forest specialist occurrence significantly correlated with natural fragments and high canopy cover. In summary, our findings corroborate a high affinity of forest specialists to natural forests. However, even modified fragments appeared suitable for the persistence of disturbance-sensitive specialist species. Our findings also indicate that small remnant patches of forest on privately owned land have significant conservation value for forest specialist birds, even when surrounded by man altered habitat.

Large-bodied birds were relatively evenly dispersed across fragments, confirming a high mobility of large-bodied species at a landscape scale (Spiegel and Nathan 2007). Additionally, body mass was positively associated with agricultural fragments and fragment size in the fourth-corner analysis, indicating that large-sized birds were able to reach isolated patches within a hostile agricultural matrix, but preferred larger fragments as destination for their among-patch flights. In contrast, body mass correlated negatively with forested gardens. This could be explained by the high proportion of small-sized nectarivores and granivores visiting farm gardens foraging for nectar-plants and animal fodder.

The low sensitivity of the overall forest bird community to cross the agricultural matrix might have been fostered by the relatively small distances among fragments within our studied landscape (Fig. 1). This might facilitate among-patch movements of birds even with intermediate to high dispersal abilities. A further reason explaining the large amount of transient species might be based on the historic distribution of scarp forests. During the last glacial maximum, scarp forests presumably persisted in small and isolated refugia that thereafter, expanded in size (Eeley et al. 1999), strongly determined by the sharp orographic conditions of the environment. Consequently, the scarp forest fauna and flora may show an evolutionary adaptation to a rather patchy forest occurrence, which might lessen their vulnerability to the present anthropogenic fragmentation. However, the actual velocity and the strength of forest loss and agricultural intensification have outreached any past scenarios. Land-use change is currently the most severe impact on the entire scarp forest diversity (Eeley et al. 1999) and thus, an alarming cause for concern.

Only a small fraction of the overall community, namely 18 species, was assumed to permanently persist in the fragments. Although a low species number can lessen the power of fourth-corner analysis (Dray and Legendre 2008; Brind'Amour et al. 2011), we were still able to detect significant trait-environment relationships in the within-patch community. Overall, our findings coincide with various studies from the Amazonian basin showing that in particular understorey, small-sized and disturbance-tolerant species with small home ranges and low niche requirements are able to persist in fragmented forests (Stouffer and Bierregaard 1995; Lees and Peres 2008; Lees and Peres 2009). Although body mass was not significantly correlated to a particular forest type, mean body mass of the within-patch species was much lower compared to the mean body mass of the among-patch community (within-patch: 21.8 g ± 2.9, among-patch: 97.7 g ± 29.8). The most abundant bird that we found persisting in the fragments was the Green-backed camaroptera (*Camaroptera brachyuran*), a small understorey insectivore, endemic to eastern South Africa and Mozambique (Hockey et al. 2005). The fact that this species is described as a forest specialist, highly sensitive to human disturbance (Hockey et al. 2005) once again, underlines the high habitat quality of forest remnants within our study area. In conclusion, we could show that although only few bird species were permanent "residents", natural and modified fragments may well comply with the requirements of generalist as well as specialist species.

Conclusion and implication for conservation

All in all, we detected a remarkably high flexibility of birds of different functional groups moving and persisting in the heterogeneous landscape of our study region. At the same time we clarify that even modified, but structurally rich and connected forest fragments, may provide valuable stepping-stones and permanent habitat for a diverse bird assemblage comprising transient species as well as "resident" birds. This is of major importance as the maintenance of high bird richness in fragmented landscapes may enhance ecological services, such as pollination, seed dispersal and pest control, which finally, are pivotal to sustain overall ecosystem functionality. We advise conservation managers to protect structurally rich forest patches, located in close proximity to each other to maintain regional bird diversity in highly fragmented landscapes.

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V. Summary

Land-use change is a major threat to forest ecosystems worldwide. Therefore, understanding the effects of human forest modification on biodiversity is an important task for conservation ecologists. The main objective of my dissertation was to evaluate how different intensities of forest modification contribute to the maintenance of species diversity and ecosystem functionality in a human-modified landscape. For this purpose, I based my studies in a heterogeneous landscape around two nature reserves, Vernon Crookes and Oribi Gorge, in KwaZulu-Natal, South Africa. I selected six most representative types of scarp forest modification – ranging from continuous forest and natural forest fragments in nature reserves to fragments within plantations and agricultural matrix, forested gardens, and secondary forest. In a total of 36 study sites, I assessed flower-visiting insects using insect traps and recorded local bird assemblages with point counts. Further, I observed flower visitation and seed removal on the native and widespread tree *Celtis africana* (Ulmacea) to analyse whether forest modification affects pollination and seed dispersal services. To assess how forest configuration affects the dispersal of animals, I carried out an in-depth study on the movement behaviour of bird assemblages within and among forest patches in the Vernon Crookes region. By means of direct observations and bird mist-netting, I followed up bird movements across nine forest fragments belonging to three different forest types. In all these three projects I give special attention to the responses of the different functional groups of a species community.

The richness of flower-visiting insects, community composition and flower visitation on *C. africana* differed significantly among the different forest types and between two study seasons in 2009 and 2010. Both flower visitor richness and flower visitation rates were strongly enhanced in the human-modified forests. This could be explained by a high abundance of large-bodied pollinators in these sites. In particular, feral honey bees (*Apis mellifera*) played a major role in the pollination of *C. africana* trees located in forest fragments within plantations and agriculture, forested gardens and secondary forests. However, effective fruit set of *C. africana* was not enhanced by an increase of flower visitation, possibly due to the tree's capability of wind pollination. This implies that even though forest modification can strongly alter insect assemblages, pollination services for trees with unspecialized flowers may remain resilient at a landscape scale.

Bird species richness was not significantly different among forest types. However, I found a significant increase in bird abundance in modified forests. In particular, fragments within agriculture, forested gardens, and secondary forests attracted a large number of forest generalists, shrubland and open country species. The abundance of forest specialists however, was much lower in modified forests. Changes in the composition of bird functional groups were also confirmed by multivariate analysis, which clearly separated bird communities by forest type. I found the highest abundance of frugivores visiting *C. africana* in natural forest fragments, fragments within agriculture, forested gardens and secondary

forests. That was also true for the estimated total fruit removal per *C. africana* tree, even though the differences among the forest types were not significant. In summary, I could show that overall bird abundance and seed removal services can be enhanced in modified forests. However, the results also underline the importance of protected natural forest for bird specialist species sensitive to human disturbance.

I found a very high movement activity of the overall bird community among the nine forest fragments that was significantly structured by bird functional groups. Especially, frugivorous birds, forest specialists and large-bodied species showed the highest dispersal abilities across the landscape. These results might be facilitated by overall high fragment quality, providing food and shelter, as well as the close proximity among the forest fragments within the landscape. Yet, a fourth-corner analysis revealed that even though modified forests were rather attractive to frugivores, forest specialists as well as large-bodied species, there was still a high affinity of the latter functional groups to natural forest fragments, close canopy cover and large fragment size. Only a small proportion of the overall bird community was recorded to steadily persist in the forest fragments. In particular, patches in the agricultural landscape were frequently used by resident insectivores and forest generalists. Ultimately, these findings suggest that remnant forest fragments may represent valuable stepping-stones as well as permanent habitat for many forest birds and thus, will help to maintain regional bird assemblages in human-modified landscapes.

Overall, my results strongly suggest that modified forests contribute to the maintenance of species diversity and ecosystem functionality in a human-modified landscape. With respect to a vast increase of human-modified forests worldwide, evidence of a high conservation potential of these habitats is encouraging news for conservation managers. In particular, modified forests that are located in close proximity to protected areas have high conservation priority as they may expand buffer zones around natural forests in human-modified landscapes. Generalizations, however, should be considered with caution. My findings strongly emphasize that human-modified forests do not completely compensate for the overall loss of natural habitat. High sensitivity of forest specialist species and overall changes in local community composition demonstrate that natural forests are essential to maintain species diversity at a larger scale. Additionally, high flexibility towards habitat changes of many species in the study region might be based on the patchy historic distribution of scarp forest that has strongly been determined by terrain and orographic conditions of the environment. Thus, it is possible that an evolutionary adaptation has lessened the vulnerability of the region's fauna and flora to the present anthropogenic forest fragmentation. Ultimately, most of the forest types in the study region are characterized by high habitat quality, including for example resource availability, structural heterogeneity and close proximity to further forest patches, so that altogether, they contribute to the high species diversity. Consequently, the maintenance of structurally rich forest habitat is

essential to maintain species diversity and ecological functionality in human-modified landscapes.

VI. Future perspectives

The results of my thesis show that modified forests may contribute to the maintenance of insect and bird richness and their ecological services in a human-modified landscape. Certainly, my projects elucidate only some of the questions that rise in the context of human forest modification and many more approaches are conceivable to further investigate the effects of anthropogenic impact on forest ecosystems. For instance, many studies have considered that not high species richness *per se* but rather functional diversity is important for long-term ecosystem stability (Tilman et al. 1997; Diaz and Cabido 2001). Therefore, it will be worthwhile to analyse the functional changes of communities due to forest modification in more detail. Recently, three promising metrics have been identified that measure independent components of functional diversity of a community: functional richness, functional evenness and functional divergence (Mason et al. 2005; Villeger et al. 2008; reviewed in Mouchet et al. 2010). While functional richness represents the amount of functional space occupied by a species community, functional evenness corresponds to the regularity of species' abundance within this space. Finally, functional divergence measures how species abundances depart from the centre of the functional space (Villeger et al. 2008; Villeger et al. 2010). Functional evenness and divergence are independent measures that are not directly related to species richness (Mouchet et al. 2010). This gives the opportunity to test different facets of species' functional diversity in a comprehensive and robust way (Mason et al. 2008).

The data obtained from bird mist-netting and movement observations (see chapter **IV**) provide an excellent basis for such an analysis. Different morphometric measurements can be used to quantify the functional diversity of communities. Thereby, I will consider traits "that influence [...] species' responses to environmental conditions" (Hooper et al. 2005), comprising overall resource use (e.g., measured as body mass), dietary specialization (e.g., gape width and culmen length), and dispersal ability (e.g., length of wing, tarsus and tail). Previous studies have shown an overall reduction in functional trait diversity due to habitat degradation (e.g., Flynn et al. 2009; Bihn et al. 2010). Using the framework of functional richness, evenness and divergence will provide a complex and elaborate tool to understand how habitat modification affects the functional diversity of species assemblages at a landscape scale.

In my dissertation I investigated the effects of land-use change on mutualistic interactions, namely pollination and seed dispersal. However, antagonistic interactions among plants, insects and birds are equally important for forest ecosystem functionality. Insectivorous birds for instance provide essential pest control services in forests (Van Bael et al. 2003). Therefore, human impact on local bird communities may cause cascading effects on both herbivorous insect and plant communities. Beside land-use intensification, climatic change has been proposed to be the main driver that will globally threaten individual species and their biotic interactions (Parmesan and Yohe 2003; Walther 2010). However, the effects

of climatic change on biodiversity are difficult to assess as steady changes in temperature, humidity and the occurrence of extreme climatic events are only expected in the long-term future. Serious effects of climate change on ecosystems have already been detected in temperate regions. For instance, climate warming has caused severe phenological changes in deciduous temperate forests (Walther et al. 2002). The development of herbivorous insects in European deciduous forests has shifted towards an early date as a response to warmer spring temperatures (e.g., reviewed in Visser and Both 2005). This short insect burst is of particular importance for many insectivorous forest birds. Phenological changes however, cause a trophic mismatch between insect development and the arrival of insectivorous birds from their wintering grounds (Both 2006). In particular long-distance migrants can hardly react to a shifted food peak. Therefore, phenological mistiming has been proposed to increasingly threaten migrant species across Europe (Moller et al. 2008; Both et al. 2010).

So far, there is little knowledge on how these phenological changes affect multitrophic interactions within bird and insect communities (but see Both et al. 2009). Furthermore, we lack studies that incorporate the effects of land-use change on these complex multitrophic cascades. Therefore, I would like to focus in prospective studies on the synergism of climate and land-use change on bird and insect communities and their multitrophic interactions along a land-use gradient in central European forests. Several questions can be raised in this context: Does the current decline of long-distance migrants lead to an increase of insect populations that strengthen herbivory in deciduous forests? Can we expect an increase of other predatory species, either from the bird or insect community that constrain potential herbivore pest outbreaks? And finally, how do the multitrophic interactions in deciduous forests differ along a land-use gradient across Europe? As both climate and land-use changes will further escalate in the near future, understanding the effects of multiple stressors on the complex interactions among species within communities will be essential to understand the magnitudes of future global change.

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VII. Zusammenfassung

Global werden Waldökosysteme durch den fortschreitenden Wandel menschlicher Landnutzung bedroht. Es ist daher von zentraler Bedeutung, die Auswirkungen anthropogener Eingriffe auf die Biodiversität und Ökosystemfunktionen von Wäldern zu erforschen. In der vorliegenden Arbeit analysierte ich, inwiefern unterschiedlich stark vom Menschen modifizierte Wälder zum Erhalt von Artenreichtum und ökosystemarer Funktionalität in anthropogen geprägten Südafrikanischen Landschaften beitragen. Alle Untersuchungen wurden in subtropischen Hangwäldern („scarp forests“) in den Schutzgebieten Oribi Gorge und Vernon Crookes und deren Umgebung in der Provinz KwaZulu-Natal durchgeführt. Ich wählte sechs für die Region typische Formen menschlicher Waldmodifikation. Diese reichten von kontinuierlichen Wäldern und natürlichen Waldfragmenten in Schutzgebieten bis hin zu Fragmenten in einer Matrix aus Eukalyptusplantagen und Zuckerrohrfeldern, bewaldeten Farmgärten und Sekundärwäldern in Wildparks. In insgesamt 36 Untersuchungsflächen erfasste ich die Diversität blütenbesuchender Insekten mit Insektenfallen und nahm die Vogeldiversität mit Punktstopp-Zählungen auf. Ferner beobachtete ich die Aktivität von Blütenbesuchern und fruchtfressenden Vögeln an der einheimischen Baumart *Celtis africana* (Ulmaceae), um zu untersuchen, ob Waldmodifikation die ökosystemaren Dienstleistungen Bestäubung und Samenausbreitung beeinflusst. In einer weiteren Studie untersuchte ich die lokalen Bewegungsmuster von Vogelgemeinschaften zwischen modifizierten Waldfragmenten in der Region um Vernon Crookes. Mit Hilfe von direkten Flugbeobachtungen und Netzfängen verfolgte ich die Bewegungen von Vögeln zwischen neun Fragmenten in drei unterschiedlich modifizierten Waldtypen. In allen Projekten untersuchte ich in besonderem Maße die Reaktionen verschiedener funktioneller Gruppen einer Artengemeinschaft auf die anthropogene Waldmodifikation.

Der Artenreichtum und die Artenzusammensetzung blütenbesuchender Insekten sowie die Blütenbesuche an *C. africana* unterschieden sich zwischen den Waldtypen und zwei aufeinanderfolgenden Untersuchungsjahren. Besonders in modifizierten Wäldern waren Artenreichtum und Besuchsraten erhöht, aufgrund einer starken Abundanz besonders großer Insekten. Vor allem die Honigbiene (*Apis mellifera*) spielte eine wichtige Rolle für die Bestäubung von *C. africana* in Waldfragmenten in Eukalyptusplantagen und Zuckerrohrfeldern, bewaldeten Gärten und Sekundärwäldern. Die erhöhten Besuchsraten steigerten den effektiven Samenansatz von *C. africana* jedoch nicht, möglicherweise bedingt durch die Fähigkeit der Baumart zur Windbestäubung. Diese Ergebnisse weisen darauf hin, dass Bestäubungsprozesse an Bäumen mit unspezialisierten Blüten - trotz veränderter Insektengemeinschaften in modifizierten Wäldern - aufrecht erhalten werden können.

Die Waldtypen unterschieden sich nicht im Artenreichtum ihrer Vogelgemeinschaften. Jedoch zeigte sich ein signifikanter Anstieg der Vogelabundanz in modifizierten Wäldern. Insbesondere Waldfragmente in Zuckerrohrfeldern, bewaldeten

Gärten und Sekundärwäldern wurden von vielen Waldgeneralisten und Offenlandarten aufgesucht. Waldspezialisten hingegen waren in modifizierten Wäldern sehr selten. Multivariate Analysen bestätigten die Verschiebungen in der Zusammensetzung von funktionellen Gruppen entlang des Störungsgradienten. Ich beobachtete die höchsten Abundanzen fruchtfressender Vögel an *C. africana* in natürlichen Waldfragmenten, Fragmenten in Zuckerrohrfeldern, bewaldeten Gärten und Sekundärwäldern. Dort waren auch die geschätzten Fraßraten von *C. africana* Früchten am höchsten, jedoch unterschieden sich diese nicht signifikant zwischen den Waldtypen. Insgesamt weisen diese Ergebnisse auf eine erhöhte Vogelabundanz sowie erhöhte Fruchtfraßraten in modifizierten Wäldern hin. Dennoch verdeutlicht die Studie auch die Bedeutung geschützter Wälder als Rückzugsräume für spezialisierte Vogelarten.

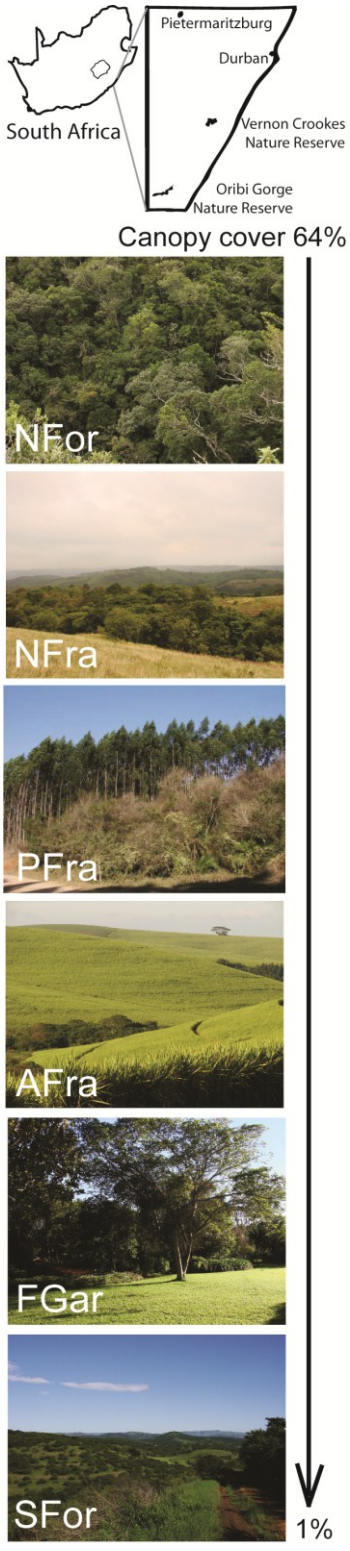
Die sehr hohe Bewegungsaktivität der Vogelgemeinschaft zwischen den neun Waldfragmenten war stark durch unterschiedliches Verhalten funktioneller Gruppen strukturiert. Besonders fruchtfressende Arten, Waldspezialisten und große Vögel zeigten eine hohe Ausbreitungsfähigkeit in der fragmentierten Landschaft. Die Nähe der Fragmente zueinander sowie deren gute Habitatqualität könnten die große Flexibilität auch spezialisierter Vogelarten erklären. Eine „fourth-corner“ Analyse zeigte dennoch, dass fruchtfressende Arten, Waldspezialisten und große Vögel eine starke Affinität zu natürlichen Fragmenten, geschlossenem Kronendach und großen Fragmenten hatten. Nur ein kleiner Teil der Vogelgemeinschaft schien in den Fragmenten sesshaft zu sein. Besonders insektenfressende und generalistische Vogelarten bewohnten die Waldfragmente in Zuckerrohrfeldern. Meine Ergebnisse zeigen, dass Waldfragmente in heterogenen Landschaften zum einen als wichtige Trittsteine für mobile Arten, zum anderen aber auch als Rückzugsraum standorttreuer Arten fungieren. Somit können auch modifizierte Wälder zum Erhalt der regionalen Vogelvielfalt in vom Menschen geprägten Landschaften beitragen.

Zusammenfassend lässt sich feststellen, dass modifizierte Wälder durchaus zum Erhalt von Artenvielfalt und ökosystemarer Funktionalität in heterogenen Landschaften beitragen. Vor dem Hintergrund der weltweiten Zunahme anthropogener Einflüsse auf Wälder, ist besonders aus naturschutzfachlicher Sicht ein hohes Potential modifizierter Wälder Grund zur Ermutigung. Vor allem modifizierte Wälder in räumlicher Nähe zu Schutzgebieten sollten hohe Schutzpriorität genießen, da sie als Pufferzonen für natürliche Wälder in anthropogen beeinflussten Landschaften fungieren können. Bei einer Verallgemeinerung der Ergebnisse ist jedoch Vorsicht geboten. Es zeigte sich, dass modifizierte Wälder den Verlust natürlicher Wälder nicht vollständig kompensierten. Eine hohe Sensitivität von Waldspezialisten und allgemeine Verschiebungen der Zusammensetzung von Artengemeinschaften in modifizierten Wäldern machten deutlich, dass natürliche Wälder essentiell für den Erhalt der Biodiversität sind. Eine zusätzliche Erklärung für die hohe Flexibilität der Artengemeinschaften gegenüber anthropogener

Waldmodifikation kann die Geschichte der Untersuchungsregion liefern. Die Tatsache, dass Hangwälder schon durch die Orographie stets voneinander isoliert vorkamen, hat möglicherweise eine evolutionäre Anpassung der Arten hervorgebracht, die die Anfälligkeit der heutigen Flora und Fauna gegenüber Fragmentierung vermindert. Schließlich zeichneten sich die Waldfragmente durch eine gute Habitatqualität aus, die durch hohe Ressourcenverfügbarkeit, strukturelle Heterogenität und kurze Distanzen zwischen den Fragmenten zu einem hohen Artenreichtum beitrug. Folglich ist der Erhalt von strukturreichen Wäldern essentiell für den Schutz von Artenvielfalt und Ökosystemfunktionen in vom Menschen modifizierten Landschaften.

VIII. Appendix

Appendix chapter II



A.1 Location of the study areas Vernon Crookes and Oribi Gorge Nature Reserve in KwaZulu-Natal, South Africa. Pictures show the six forest types: continuous natural forests (NFor), natural forest fragments (NFra), fragments within plantation (PFra), fragments within agriculture (AFra), forested gardens (FGar), and secondary forests (SFor). Forest types are ordered by decreasing canopy cover (for details see methods section).

A.2 Size classification and total abundance of the insect flower visitors recorded on *Celtis africana* in 2009 and 2010.

Morphospecies	Order	< 2 mm	2–5 mm	5–10 mm	> 10 mm	Abundance
Honey bee (Apis mellifera)	Hymenoptera				x	852
Medium black fly	Diptera			x		394
Small black fly	Diptera		x			314
Very small fly 1	Diptera	x				276
Medium hover fly	Diptera			x		121
Large wasp	Hymenoptera				x	42
Large hover fly	Diptera				x	30
Thrips	Thysanoptera	x				24
Medium wasp	Hymenoptera			x		23
Small wasp 1	Hymenoptera		x			21
Small wasp 2	Hymenoptera		x			17
Small hover fly	Diptera		x			17
Wild bee	Hymenoptera			x		13
Small beetle	Coleoptera		x			8
Very small fly 2	Diptera	x				7
Medium beetle	Coleoptera			x		6
Medium ant	Hymenoptera			x		4
Very small beetle	Coleoptera	x				4
Small ant	Hymenoptera		x			2
True bug	Hemiptera		x			2

Appendix chapter III

A.1 Bird species recorded in six different forest types: continuous natural forest (NFor), natural forest fragment (NFra), fragment within plantation (PFra), and fragment within agriculture (AFra), forest garden (FGar) and secondary forest (SFor). Categorization of forest specialists (FS), forest generalists (FG), shrubland species (SL), and open country species (OC) according to Hockey et al. (2005).

Common name	Scientific name	Habitat speciali-zation	Sum of individuals	NFor	NFra	PFra	AFra	FGar	SFor
Brown scrub robin	*Cercotrichas signata*	FS	3	x	x		x		
Chorister robin-chat	*Cossypha dichroa*	FS	5				x		x
Crowned hornbill	*Tockus alboterminatus*	FS	2		x			x	
Dark-backed weaver	*Ploceus bicolor*	FS	18	x	x		x		x
Green wood-hoopoe	*Phoeniculus purpureus*	FS	13	x	x		x	x	
Grey sunbird	*Cyanomitra veroxii*	FS	4	x			x		
Knysna turaco	*Tauraco corythaix*	FS	8	x			x		x
Lemon dove	*Aplopelia larvata*	FS	1	x					
Narina trogon	*Apaloderma narina*	FS	1	x					
Red-fronted tinkerbird	*Pogoniulus pusillus*	FS	2	x	x				
Tambourine dove	*Turtur tympanistria*	FS	1				x		
Trumpeter hornbill	*Bycanistes bucinator*	FS	5				x	x	
Yellow-rumped tinkerbird	*Pogoniulus chrysoconus*	FS	3		x	x	x		
Yellow-throated woodland warbler	*Phylloscopus ruficapilla*	FS	2		x				
African dusky flycatcher	*Muscicapa adusta*	FG	16	x		x		x	
African emerald cuckoo	*Chrysococcyx cupreus*	FG	5	x		x	x		
African green-pigeon	*Treron calvus*	FG	6					x	
African paradise-flycatcher	*Terpsiphone viridis*	FG	5					x	x
African pygmy-kingfisher	*Ispidina picta*	FG	1						x
Bar-throated apalis	*Apalis thoracica*	FG	15			x	x		x
Black cokooshrike	*Campephaga flava*	FG	4		x				x
Black cuckoo	*Cuculus clamosus*	FG	6				x		x
Black-backed puffback	*Dryoscopus cubla*	FG	6	x	x		x	x	
Black-collared barbet	*Lybius torquatus*	FG	11			x	x	x	x
Black-headed oriole	*Oriolus larvatus*	FG	40	x	x	x	x	x	x
Brown-hooded kingfisher	*Halcyon albiventris*	FG	3			x			
Burchell's coucal	*Centropus burchellii*	FG	3			x	x		x
Cape batis	*Batis capensis*	FG	7		x		x	x	
Cape white-eye	*Zosterops pallidus*	FG	57	x	x	x	x	x	x
Collared sunbird	*Hedydipna collaris*	FG	50	x	x	x	x	x	x
Dark-capped bulbul	*Pycnonotus tricolor*	FG	93	x	x	x	x	x	x

Common name	Scientific name	Habitat speciali-zation	Sum of individuals	NFor	NFra	PFra	AFra	FGar	SFor
Diderick cuckoo	*Chrysococcyx caprius*	FG	8			x		x	x
Eastern olive sunbird	*Cyanomitra olivacea*	FG	39	x	x	x	x	x	x
Fork-tailed drongo	*Dicrurus adsimilis*	FG	16	x	x	x	x	x	x
Golden-tailed woodpecker	*Campethera abingoni*	FG	1					x	
Greater double-collared sunbird	*Cinnyris afer*	FG	3					x	
Green-backed camaroptera	*Camaroptera brachyura*	FG	54	x	x	x	x	x	x
Grey cuckooshrike	*Coracina caesia*	FG	1	x					
Klaas's cuckoo	*Chrysococcyx klaas*	FG	4					x	x
Knysna woodpecker	*Campethera notata*	FG	1		x				
Lesser honeyguide	*Indicator minor*	FG	1				x		
Olive thrush	*Turdus olivaceus*	FG	11	x		x	x	x	
Pin-tailed whydah	*Vidua macroura*	FG	1				x		
Purple-crested turaco	*Gallirex porphyreolophus*	FG	3	x					x
Red-backed mannikin	*Spermestes bicolor*	FG	10			x		x	
Red-capped robin-chat	*Cossypha natalensis*	FG	5	x	x				
Red-chested cuckoo	*Cuculus solitarius*	FG	3	x			x		
Red-eyed dove	*Streptopelia semitorquata*	FG	10		x		x	x	
Red-winged starling	*Onychognathus morio*	FG	11					x	
Sombre greenbul	*Andropadus importunus*	FG	11	x			x	x	
Southern black tit	*Parus niger*	FG	1					x	
Southern boubou	*Laniarius ferrugineus*	FG	32	x	x		x		x
Speckled mousebird	*Colius striatus*	FG	6					x	x
Spectacled weaver	*Ploceus ocularis*	FG	8				x	x	x
Square-tailed drongo	*Dicrurus ludwigii*	FG	16	x	x		x	x	
Swee waxbill	*Coccopygia melanotis*	FG	1			x			
Terrestrial brownbul	*Phyllastrephus terrestris*	FG	5		x		x		
Thick-billed weaver	*Amblyospiza albifrons*	FG	6			x		x	x
Village weaver	*Ploceus cucullatus*	FG	70					x	x
Violet-backed starling	*Cinnyricinclus leucogaster*	FG	16				x	x	
Willow warbler	*Phylloscopus trochilus*	FG	1				x		
African firefinch	*Lagonosticta rubricata*	SL	1					x	
Amethyst sunbird	*Chalcomitra amethystina*	SL	41	x	x			x	
Cape glossy starling	*Lamprotornis nitens*	SL	50	x	x		x	x	x
Cape turtle-dove	*Streptopelia capicola*	SL	3					x	
Chinspot batis	*Batis molitor*	SL	2						x
Common fiscal	*Lanius collaris*	SL	3					x	

Common name	Scientific name	Habitat speciali-zation	Sum of individuals	NFor	NFra	PFra	AFra	FGar	SFor
Crested barbet	*Trachyphonus vaillantii*	SL	2					x	
House sparrow	*Passer domesticus*	SL	2					x	
Lazy cisticola	*Cisticola aberrans*	SL	18		x	x		x	x
Little bee-eater	*Merops pusillus*	SL	2						x
Red-collared widowbird	*Euplectes ardens*	SL	7		x				x
Southern black flycatcher	*Melaenornis pammelaina*	SL	10				x	x	x
Southern double-collared sunbird	*Cinnyris chalybeus*	SL	5					x	
Southern grey-headed sparrow	*Passer diffusus*	SL	6					x	
Southern mask weaver	*Ploceus velatus*	SL	1	x					
Steppe buzzard	*Buteo vulpinus*	SL	2			x			
Tawny-flanked prinia	*Prinia flavicans*	SL	4		x				x
White-browed scrub-robin	*Cercotrichas leucophrys*	SL	2						x
Yellow-fronted canary	*Crithagra mozambica*	SL	29		x	x	x	x	x
Cape weaver	*Ploceus capensis*	OC	57				x	x	x
Common house martin	*Delichon urbicum*	OC	1					x	
Common waxbill	*Estrilda thomensis*	OC	13						x
Croaking cisticola	*Cisticola natalensis*	OC	3		x				x
Hadeda ibis	*Bostrychia hagedash*	OC	5				x	x	
Lesser swamp-warbler	*Acrocephalus gracilirostris*	OC	2						x
Long-tailed widowbird	*Euplectes progne*	OC	4		x				x
Southern red bishop	*Euplectes orix*	OC	1						x
Wing-snapping cisticola	*Cisticola ayresii*	OC	1						x
Yellow-throated longclaw	*Macronyx croceus*	OC	1		x				

A.2 Observed and estimated bird species richness of the six forest types using different diversity estimators (standard errors are given for Chao 2). Continuous natural forest (NFor), natural forest fragment (NFra), fragment within plantation (PFra), and fragment within agriculture (AFra), forest garden (FGar) and secondary forest (SFor).

Forest type	Observed species richness	Chao 2	ICE	MMMeans	Richness recorded according to estimators (%)
NFor	29	45.7 ± 9.7	53.3	47.1	54–62
NFra	32	46.2 ± 8.1	56.1	54.3	57–69
PFra	22	33.5 ± 8.1	36.3	33.0	61–67
AFra	40	55.9 ± 8.2	72.7	64.6	55–72
FGar	47	68.1 ± 10.2	76.2	73.3	62–69
SFor	41	62.4 ± 10.5	75.3	66.1	54–66

Appendix chapter IV

A.1 Classification of bird species into among- and within-patch community based on observed movements (o) and mist-net captures (c). Recaptures were separated into to birds that dispersed from their original ringing site (reo) and birds that were recaptured at the same forest patch (res). frug = frugivore, insec = insectivore, omni = omnivore, nect = nectarivore, gran = granivore, carn = carnivore, FS = forest specialist, FG = forests generalist, SL = shrubland species, OC = open-country species.

Species	Among-patch	Within-patch	Mass	Habitat	Diet
African dusky flycatcher *Muscicapa adusta*	o,c,res		12.1	FG	insec
African firefinch *Lagonosticta rubricata*	o,c,res		10.2	SL	gran
African goshawk *Accipiter tachiro*	c,reo		227.1	FS	carn
African green-pigeon *Treron calvus*	o		247.0	FG	frug
African paradise-flycatcher *Terpsiphone viridis*	o,c		14.5	FG	insec
African pied wagtail *Motacilla aguimp*	c		33.9	OC	insec
African pygmy-kingfisher *Ispidina picta*	c	res	13.9	FG	insec
African reed-warbler *Acrocephalus arundinaceus*	c	res	10.0	OC	insec
African stonechat *Saxicola torquatus*	c		15.1	OC	insec
Amethyst sunbird *Chalcomitra amethystina*	o,c		14.1	SL	nect
Ashy flycatcher *Muscicapa caerulescens*	c	res	16.6	FG	insec
Barn swallow *Hirundo rustica*	c		17.1	OC	insec
Barratt's Warbler *Bradypterus barratti*	c		17.4	FS	insec
Bar-throated apalis *Apalis thoracica*	c	res	10.4	FS	insec
Black cuckooshrike *Campephaga flava*	o,c		34.2	FG	insec
Black saw-wing *Psalidoprocne holomelas*	c		11.6	FG	insec
Black sparrowhawk *Accipiter melanoleucus*	c		980.0	FG	carn
Black-backed puffback *Dryoscopus cubla*	o,c,res		28.8	FG	insec
Black-bellied starling *Lamprotornis corruscus*	o,c,reo		59.6	FS	frug
Black-collared barbet *Lybius torquatus*	o,c,res		57.8	FG	frug
Black-headed oriole *Oriolus larvatus*	o,c		76.6	FG	omni
Blue-mantled crested-flycatcher *Trochocercus cyanomelas*	c		9.8	FS	insec
Bokmakierie *Telophorus zeylonus*	o		61.2	SL	insec
Brimstone canary *Chritagra sulphurata*	o		18.2	FG	frug
Bronze mannikin *Spermestes cucullata*	o,c,res		10.4	SL	gran
Brown scrub-robin *Cercotrichas signata*	c	res	33.9	FS	insec
Brown-backed honeybird *Prodotiscus regulus*	c		13.5	FG	insec
Brown-hooded kingfisher *Halcyon albiventris*	c		63.5	FG	insec
Buff-spotted flufftail *Sarothrura elegans*	c		49.9	FS	insec
Cape batis *Batis capensis*	c	res	11.5	FS	insec
Cape glossy starling *Lamprotornis nitens*	o,c,res		89.5	SL	omni
Cape grassbird *Shenoeacus afer*	c		34.5	OC	insec
Cape robin-chat *Cossypha caffra*	c	res	27.7	FG	insec
Cape wagtail *Motacilla capensis*	c		21.9	OC	insec
Cape weaver *Ploceus capensis*	c		52.5	OC	omni
Cape white-eye *Zosterops pallidus*	o,c,res		11.2	FG	omni
Chinspot batis *Batis molitor*	o,c		11.6	SL	insec
Chorister robin-chat *Cossypha dichroa*	c	res	42.7	FS	omni
Collared sunbird *Hedydipna collaris*	o,c,res		7.1	FS	nect
Common waxbill *Estrilda thomensis*	o,c		8.9	OC	gran
Croaking cisticola *Cisticola natalensis*	c	res	27.7	OC	insec

Species	Among-patch	Within-patch	Mass	Habitat	Diet
Crowned hornbill *Tockus alboterminatus*	o,c		245.7	FG	omni
Dark-backed weaver *Ploceus bicolor*	o,c,res		35.0	FS	insec
Dark-capped bulbul *Pycnonotus tricolor*	o,c,res		42.9	FG	frug
Drakensberg prinia *Prinia hypoxantha*	c		11.1	OC	insec
Eastern olive sunbird *Cyanomitra olivacea*	o,c,reo,res		12.0	FS	nect
Emeral-spotted wood-dove *Turtur calcospilos*	c		63.6	FG	omni
Fan-tailed widowbird *Euplectes axillaris*	c		29.1	OC	gran
Forest canary *Crithagra scoptos*	o,c,reo		14.3	FS	gran
Fork-tailed drongo *Dicrurus adsimilis*	o,c		48.2	FG	insec
Golden-tailed woodpecker *Campethera abingoni*	c		70.0	FG	insec
Greater double-collared sunbird *Cinnyris afer*	o,c,res		11.6	FG	nect
Green wood-hoopoe *Phoeniculus purpureus*	o,c		70.3	FG	insec
Green-backed camaroptera *Camaroptera brachyura*	c	res	12.0	FS	insec
Grey cuckooshrike *Coracina caesia*	o,c		52.5	FS	insec
Grey sunbird *Cyanomitra veroxii*	c		11.4	FG	nect
Grey waxbill *Estrilda perreini*	c		7.6	FS	gran
Hadeda bis *Bostrychia hagedash*	o,c		1455.0	OC	insec
House sparrow *Passer domesticus*	o,c		24.2	SL	omni
Klaas's cuckoo *Chrysococcyx klaas*	c	res	29.0	FG	insec
Knysna turaco *Tauraco corythaix*	o,c		299.8	FS	frug
Lazy cisticola *Cisticola aberrans*	c	res	13.2	SL	insec
Lemon dove *Aplopelia larvata*	c		159.1	FS	frug
Lesser honeyguide *Indicator minor*	o,c,reo,res		29.8	FG	insec
Lesser striped swallow *Hirundu abyssinica*	o,c,res		17.8	OC	insec
Little rush-warbler *Bradypterus baboecala*	c		15.1	OC	insec
Little sparrowhawk *Accipiter minullus*	c		80.6	FG	carn
Little swift *Apus affinis*	c	(res)	28.3	OC	insec
Narina trogon *Apaloderma narina*	c		73.3	FS	insec
Neddicky *Cisticola fulvicapilla*	c		10.3	SL	insec
Olive bush-shrike *Telophorus olivaceus*	c		30.8	FS	insec
Olive thrush *Turdus olivaceus*	o,c,reo,res		92.9	FG	insec
Olive woodpecker *Dendropicos griseocephalus*	c	res	54.9	FS	insec
Pin-tailed whydah *Vidua macroura*	o,c,res		16.0	SL	gran
Red-backed mannikin *Spermestes bicolor*	o,c,reo,res		10.1	FG	gran
Red-capped robin-chat *Cossypha natalensis*	c,reo	res	32.0	FG	insec
Red-chested cuckoo *Cuculus solitarius*	c		84.4	FG	insec
Red-eyed dove *Streptopelia semitorquata*	o,c		233.0	FG	gran
Red-fronted tinkerbird *Pogoniulus pusillus*	c		14.2	FG	frug
Red-winged starling *Onychognathus morio*	o,c		130.0	FG	omni
Scaly-throated honeyguide *Indicator variegatus*	c,reo		50.9	FS	omni
Sombre greenbul *Andropadus importunus*	o,c,reo,res		34.5	FG	frug
Southern black flycatcher *Melaenornis pammelaina*	o,c		33.5	SL	insec
Southern black tit *Parus niger*	o,c		23.8	FG	insec
Southern boubou *Laniarius ferrugineus*	o,c,res		55.1	FG	omni
Southern double-collared sunbird *Cinnyris chalybeus*	o,c		7.7	FS	nect
Southern grey-headed sparrow *Passer diffusus*	c		26.0	SL	gran
Southern red bishop *Euplectes orix*	c		17.9	OC	gran
Southern tchagra *Tchagra tchagra*	c		48.6	SL	omni
Speckled mousebird *Colius striatus*	o,c		50.4	FG	frug
Spectacled weaver *Ploceus ocularis*	o,c,reo,res		28.3	FG	insec
Square-tailed drongo *Dicrurus ludwigii*	o,c		29.6	FS	insec
Streaky-headed seedeater *Chritagra gularis*	o,c		20.0	FG	omni
Tambourine Dove *Turtur tympanistria*	o,c		70.9	FS	gran
Tawny-flanked prinia *Prinia flavicans*	c	res	9.4	SL	insec

Species	Among-patch	Within-patch	Mass	Habitat	Diet
Terrestrial brownbul *Phyllastrephus terrestris*	c	res	39.3	FG	insec
Thick-billed weaver *Amblyospiza albifrons*	o,c		40.2	FG	gran
Trumpeter hornbill *Bycanistes bucinator*	o,c		620.0	FS	omni
Village weaver *Ploceus cucullatus*	o,c,reo		37.1	FG	omni
Violet-backed starling *Cinnyricinclus leucogaster*	o,c		49.1	FG	frug
White-bellied sunbird *Cinnyris talatala*	o,c		8.2	SL	nect
White-rumped swift *Apus caffer*	c	(res)	25.4	OC	insec
White-starred robin *Pogonocichla stellata*	c	res	20.1	FS	omni
Willow warbler *Phylloscopus trochilus*	c		8.0	FG	insec
Yellow weaver *Ploceus subaureus*	c		31.9	OC	omni
Yellow-billed kite *Milvus aegypticus*	o		807.0	OC	carn
Yellow-fronted canary *Crithagra mozambica*	o,c		13.1	SL	gran
Yellow-throated petronia *Petronia superciliaris*	o		27.1	SL	omni
Yellow-throated woodland-warbler *Phylloscopus ruficapilla*	c	res	7.3	FS	insec

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Ausbildung

seit 08/2008	Promotion bei Frau Jun.–Prof. Dr. Nina Farwig, Naturschutzökologie, Philipps-Universität Marburg
10/2002 – 03/2008	Studium der Diplombiologie, Philipps-Universität Marburg Schwerpunkte: Naturschutz, Pflanzenökologie, Botanik Diplomarbeit bei Prof. Dr. Birgit Ziegenhagen, Naturschutzbiologie, zum Thema „Species crossability relationships and hybrid performance of riparian willows“
08/1995 – 07/2002	Gymnasium Lüchow – Landkreis Lüchow-Dannenberg Abschluss mit Abitur
09/1989 – 06/1995	Grundschule Gartow – Landkreis Lüchow-Dannenberg

Stipendien und Preise

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08/2009	Maria Sibylla Merian Preis der „Gesellschaft für Tropenökologie“ in der Kategorie „Beste Redebeiträge“

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Erklärung

Ich versichere, dass ich meine Dissertation

> "Modified forests are vital for species communities and ecological functionality in a heterogeneous South African landscape"

selbständig und ohne unerlaubte Hilfe angefertigt habe und mich keiner als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe. Diese Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg /Lahn, im August 2011

Eike Lena Neuschulz